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By LEVERETT ALLEN ADAMS

Introduction to the Vertebrates

Second Edition

C O M P A R A T I V E A N A T O M Y

An Introduction To The Vertebrates

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P R E F A C E

This book replaces the "Introduction to the Vertebrates" written in 1933 and revised in 1938 by the senior author. New discoveries and viewpoints have made it necessary to rewrite most of the text and change the title. The idea of making the book more usable for a wide variety of vertebrate courses has been foremost in the minds of the writers. The original arrangement has been changed, the book being in two instead of three sections as in the original. This was accomplished by incorporating the material formerly in the third sections into the first two sections.

The first part of the book is a review of the classification of the different groups of the vertebrates. This part may serve as a review for those students who have already had an elementary course and are now starting the study of comparative anatomy, or it may serve as an introduction to the vertebrates for those students who have had but little experience with this group. One of the necessary tasks for any student in a new subject is to acquire a mastery of the vocabulary, which in the field of vertebrate anatomy is not particularly easy. Consequently, a fairly comprehensive glossary containing short definitions of common terms is included to help the elementary student.

The second and major part of the book is devoted to comparative study of the organ systems of the vertebrates. Some sections have been expanded and may contain more material than the student can cover in one semester. However, it is arranged so that the instructor may omit any parts desired, leaving the remainder as a source for future reference. Most of the systems are treated by a general comparison of each part or organ in the different classes of vertebrates and are followed by a description of the systems as they occur in each class. This involves some repetition which the authors feel is justified by the value of offering two viewpoints to emphasize the evolution of the various systems.

In numerous instances, it has seemed advisable to enlarge sections of the book, since the material was found inadequate or too scanty. Other chapters have been somewhat reduced in size by eliminating repetitions and shortening statements. Because of well-established changes made recently in classification, it was necessary to make some major alterations in the arrangement of certain groups. Full advantage

has been taken of the significant work of Professor A. S. Romer, especially in the rearrangement of the fishes, amphibians, and reptiles.

Numerous changes have been made in the illustrations to correct errors, and an appreciable number of new illustrations have been added.

The main part of the revision has fallen on the shoulders of the junior author, and he is responsible for many changes made in the format of the book, the arrangement of the material, and many additions and corrections. Through his collaboration, practically every page of the old book has been revised, corrected, and brought up to date.

We wish to express our appreciation for the assistance given by Professor R. K. Enders of Swarthmore College, who made many suggestions, gave some new ideas concerning the treatment of several chapters, and supplied some illustrations. Professor Harley N. Gould of Sophie Newcomb College offered many helpful suggestions and criticisms. We are greatly indebted to the many colleagues who have read and criticised various sections of the book.

Lastly we wish to express our appreciation of the fine attitude of the publishers who have gone more than half way in helping with the many problems that arise in publishing a book.

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P A R T O N E

A Review of the Vertebrates

CHAPTER ONE

Introduction

Lamarck (1744–1829) made the first scientific division of the animal kingdom into two parts, calling one the Vertebrata and the other the Invertebrata. This is a very convenient division, and it is rather easy to place in one group all animals that have a vertebral column and in another group all that do not. Some of the invertebrates, such as the insects and certain snails, starfish, and sponges, have an exoskeleton, formed by cell secretions on the outside of the body, but not made up of specialized cell structures like the internal skeleton of the vertebrates. After the time of Lamarck there was discovered an intermediate group of small animals living in the sea which did not fit into his classification. They are related to the vertebrates but have a more simple structure. When it was found that this intermediate group, now known as the protochordates, had no vertebrae, it was necessary to make a new classification that would include all these related animals with the vertebrates. This new division, or phylum, was given the name *Chordata* by Balfour in 1880. The name Vertebrata was retained as a subphylum, and the lower forms, or protochordates, were divided into three other subphyla known as the Hemichordata, the Urochordata, and the Cephalochordata.

All members of the phylum Chordata have three characteristic structures: (1) an internal axial skeleton of some kind, (2) a series of pharyngeal gill slits, and (3) a tubular central nerve cord that is dorsal to the digestive tube. These three structures are present in some stage of the development of every chordate.

The primitive axial skeleton of the chordates is the *notochord*, an elastic rod that lies between the spinal cord and the digestive tube and usually extends from the head region to the tip of the tail, though it reaches only to the ear region in the embryos of vertebrates. It acts as a stiffening rod and gives the animal an advantage in the use of the segmental muscles. Nothing similar is found in other phyla, although a strand of fibers in the annelid worms is sometimes compared with it, but with little justification. The axial skeleton of the vertebrates consists of the vertebral column and the skull.

The pharyngeal gill slits of the chordates are a series of paired openings that make their appearance at some time in the development of every member of the phylum, even in those forms that do not use them in adult life as accessories for breathing. Early in the evolution of chordates, as respiration could no longer be carried on through the skin alone, it became necessary to have some sort of openings through which water could reach the tissues that were specialized for the interchange of gases. In fishes and other water-living chordates the gill slits are the openings between the gill arches, and in animals that breathe with lungs the gill slits still appear at some stage of embryonic development.

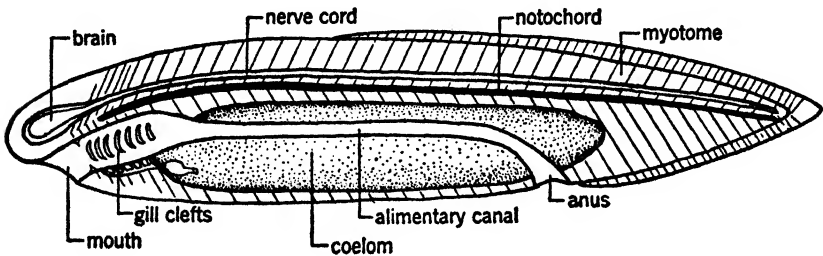


FIG. 1. Diagram showing the principal characters of a chordate.

The central nervous system of the chordates is a tubular structure that is always dorsal to the notochord and the digestive tube. It originates from the outer germ layer, or ectoderm, in the embryo. It appears along the median line of the back, first as a narrow plate, then a groove, and finally a tube, which separates from the parent ectoderm and becomes the spinal cord; its anterior end may be enlarged to form the brain. It thus differs from the nervous system of the invertebrates, in which the nerve cords are usually paired and solid, and are either lateral or ventral. The spinal cord and the brain maintain their dorsal position and their dominating relationships to other structures throughout the vertebrates.

Chordates

At the foot of the chordate tree are several subphyla consisting of animals living at the present day that may show something of the ancestry of the vertebrates. Of course these modern forms cannot be considered as ancestral themselves, although their early representatives might have been. All these modern protochordates are small and live in the sea. Collectively they have three primary characters in common with the vertebrates: (1) an axial skeleton, (2) pharyngeal gill slits, and (3) a dorsal tubular nervous system (Figs. 1, 4). Some of

these characters may disappear in the adults of the hemichordates and the urochordates, but all are retained in the cephalochordates. The brain is undifferentiated and, except in the cephalochordates, can

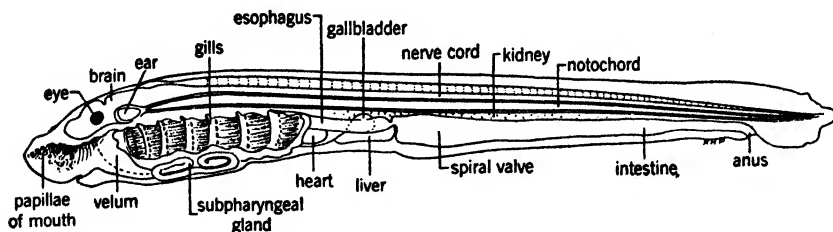


FIG. 2. Semidiagrammatic sagittal section of an ammocoetes. The ammocoetes is well adapted to serve as an illustration of an archetypal vertebrate, since it lacks the branchial atrium of *Amphioxus*, and the resulting complications. All its structures are simple in form and follow the plan for those of the higher vertebrates. It shows a heart, brain, ear, eye, and pituitary and thyroid glands, all of which are lacking in *Amphioxus*, but are characteristic of the vertebrates. The ammocoetes becomes especially valuable for comparison, since the relationship of the ostracoderms and the cyclostomes now appears to be firmly established. Modified from Goodrich and others.

hardly be called a brain at all. The sense organs do not appear or are poorly developed in the adult stage of these subphyla. The circulatory system, at its best, is rather incomplete, consisting of a simple tubular heart that is merely an enlarged blood vessel.

Hemichordata

The hemichordates, which have long been included in the chordates, probably constitute a separate phylum, as their so-called chordate characters are not well defined. The hemichordates, best represented by *Saccoglossus* (see Fig. 3), are small, acorn-headed, worm-like



FIG. 3. *Saccoglossus*.

animals varying in length from a few inches to several feet. Their developmental history shows some characters that would point to a relationship with the Echinodermata, since their tornaria larva may be compared with the ciliated larva of the echinoderm group. They have pharyngeal gill slits which serve for respiration by bathing the blood vessels with water. A short diverticulum from the dorsal region of the digestive tube extends into the proboscis and stiffens it to aid

in locomotion through the sand, and this has been considered comparable to the notochord of the chordates. The nervous system develops in the same manner as in the chordates, from a dorsal longitudinal groove in the ectoderm, with some suggestion of a tubular structure; but in the adult there is a ventral as well as a dorsal cord. No excretory organs have been demonstrated, although ciliated pores open to the exterior from the region of the collar, connecting with a region in the proboscis that is richly supplied with blood vessels and may be compared to a glomerulus. The sexes are separate, the gonads opening to the exterior through the body wall (Fig. 3).

Subphylum Urochordata

The urochordates (Fig. 6) are a large group of sea animals, consisting of both free-living and sessile forms. They are peculiar in that the young, or larvae, are typical chordates and are called tadpole larvae because of their resemblance to larval amphibians. The adults, whether free-swimming, sessile, or covered with cellulose tests, lose practically all their chordate characters and show much specialization and degeneracy. The notochord develops typically as in other chordates, but in adult life it practically disappears. The myotomic muscles in the tail region make it a vigorous propelling organ. The nervous system in the young is similar to that of other chordates, consisting of a tube expanded into a brain-like vesicle, an eye with a cuticular lens, and a calcareous mass representing an ear. These, however, remain only for a short period during development. A neuropore connects the brain vesicle with the exterior. In adult life the nerve structure is reduced to a small ganglion with anterior and posterior nerves and a smaller subneural ganglion which has a ciliated tubular connection with the pharynx, suggesting the hypophysis of the vertebrates. The pharynx is pierced by gill slits, usually two pairs in the young, but in the adults these are increased in number and strengthened and protected by a series of gill bars. In adults of the sessile forms the pharynx remains respiratory, and the rest of the digestive tube becomes an S-shaped structure with the anus near the mouth, its position being due to the covering of the animal by a test. The heart is tubular and directs the blood alternately forwards and backwards. The excretory system may consist of a series of vesicles placed close to the intestine, but without ducts. The reproductive system is of the hermaphroditic type, the ova and spermatozoa ripening at different times and passing through openings into the cloaca. The urochordates offer little that would help in solving the problem of the origin of the chordate stem, but they constitute a highly specialized and degenerate group with unquestioned affinities to the cephalochordates (Fig. 7).

Subphylum Cephalochordata

The lancelets, represented by *Amphioxus* (*Branchiostoma*, Fig. 7), consist of a small number of species and genera which are found along the coasts of many parts of the world, living near the shore and burrowing in the sand for protection. In parts of China they form a staple food at certain seasons of the year. They are chordates stripped of all but the bare essentials, and although they may supply interesting facts regarding chordate ancestry, they are modern forms and can hardly be looked upon as more than degenerate examples of a group that may have been an ancestral type. Their notochord, originating as a longitudinal dorsal ridge from the endoderm and extending from the nose to the tip of the tail, serves as a stiffening rod which with the myotomic muscles gives ample means of locomotion. The notochord is covered by two sheaths, the outer of which covers the nerve cord also. There are suggestions of skeletal material in other parts of the body; for example, in the oral hood there is a ring of a gelatinous material forming a delicate set of rods, with a series of rods extending into the cirri, and the pharyngeal region is also surrounded by a branchial basket formed of similar rods. The tail fin has a series of small supports formed by concentration of connective tissue. The nerve cord has a position typical of the chordates, being dorsal to the notochord and digestive systems. The brain, a slight modification of the nerve tube, is thin-walled and has an eye-spot between the first two cranial nerves. Its ventral diverticulum may be an infundibulum. In early development a neuropore opens from the neural canal. Segmental nerves arise from the cord, but the dorsal and ventral roots are unequal in number and do not unite as in vertebrates, nor do the nerves arise opposite to one another. It has been shown that the dorsal nerves carry motor as well as sensory fibers. The segmental nerves have no ganglia, and no autonomic system has been differentiated. The numerous gill slits, often numbering as many as fifty pairs, are supplied with cartilaginous bars which form a branchial basket suggesting that of the vertebrates. The clefts are covered by a fold of the body, the outlet being an atrial pore located considerably anterior to the anus.

Subphylum Vertebrata

The vertebrates comprise the fishes, amphibians, reptiles, birds, and mammals, and include a group of fish-like forms, the Agnatha—containing the ostracoderms and cyclostomes. Most of the vertebrate structures are not represented at all in the invertebrates. Besides the three primary characteristics of chordates, numerous other distinctive structures have appeared in the evolution of the vertebrates. Although

the subphylum Vertebrata is a well-defined group of animals, a very variable series of structures have developed associated with their many different modes of life. In a comparative study of the vertebrates, it is rather surprising to find how few entirely new structures appear between the fishes and the mammals, for almost invariably the finished structures of one class of vertebrates can be traced through earlier classes, where they can be seen in a simpler form, although they sometimes are performing an entirely different function. The first vertebrates lived in water, and their bodies were suited to this element; with the appearance of land vertebrates, there were striking changes in many structures. In the first amphibians, the first vertebrates to live on land, practically all the structures were present that were needed for land life, but the structures were comparatively simple for the most part. As the vertebrates advanced, the organs and other structures changed, enabling them to adjust themselves better to land life. The changes came about usually by minor modifications of structures already present, often by the addition of material borrowed from an entirely different source.

Bilateral Symmetry

Vertebrates are bilaterally symmetrical. A sagittal cut will divide the body into two equal halves, a right and a left. This bilaterality holds for all the main structures, such as the skeletal and nervous systems, and in general for the organs, although paired structures may not be exactly alike, either in size or in position. The lungs, kidneys, and reproductive organs, though paired, are not always of the same size and may be somewhat shifted in position. Bilaterality is not an exclusive vertebrate character, since it is also found in some of the invertebrate phyla.

Metamerism

Repetition of structures in a linear series is a characteristic which occurs in annelid worms, insects, in some other groups of invertebrates as well as in the chordates. The lower vertebrates are strongly segmented both externally and internally, but in the higher vertebrates there is a tendency for the external segmentation to be lost or to become unrecognizable. The internal metamerism, however, is retained and is clearly evident in the skeletal, nervous, circulatory, excretory, and other systems.

Divisions of the Body

The body of a vertebrate always shows a tendency to divide into regions—a head, a trunk, and a tail—which are more or less distinct and are adapted to separate kinds of activities. The head region at

the anterior end of the body is always characterized by the mouth, or entrance to the digestive tube, with accessory structures that aid in food-getting, such as the sense organs, jaws, and salivary glands. Even in the lowest vertebrates there is some kind of skull and jaws or a substitute. Once started, this head region continues to develop

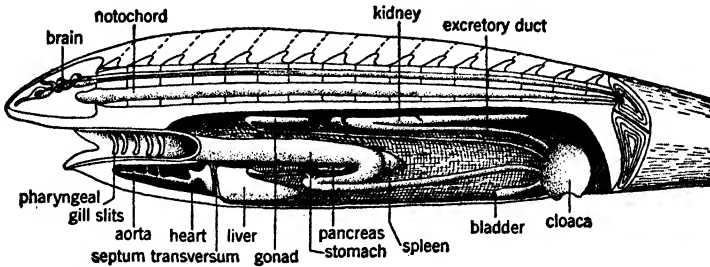


FIG. 4. Diagram to show the main characters of a primitive vertebrate.

as the vertebrates advance, and is accompanied by the gradual differentiation of the brain and sense organs. The trunk region contains all the other organs, and they are adjusted to the cavity of this region. Numerous developments have taken place in the skeletal parts of this region that protect and support these organs. In land vertebrates there is a further differentiation of the trunk into a lumbar and a sacral region. The tail region is always post-anal, since the end of the digestive tube is not terminal. The chief use of the tail in early forms is for locomotion.

The Skin and Exoskeleton

The covering of the body of the vertebrates is quite different from that of the invertebrates, since it does not develop any shell-like structures formed as cell secretions. The skin of *Amphioxus*, a protochordate, is only one cell in thickness. In vertebrates the epidermis, or outer layer of the skin, is made up of many layers of cells. It supplies several kinds of structures, such as scales, feathers, hairs, horns, and glands. The inner layer, or corium, is of mesodermal origin and contributes teeth, bony scales, abdominal ribs, and the dermal bones of the skeleton. This layer is much more complicated in structure than the epidermis, for it contains blood vessels, nerves, connective tissue fibers, lymphatics, and other material. It has made numerous contributions to the skeleton, for example, the teeth associated with the jaws and skull bones, the dermal scales or plates which finally become a part of the skull, and parts of the shoulder girdle, sternum, and fins. Most of the vertebrates have specialized coverings. Fishes with few

exceptions have scales or plates, the ancient fishes having been supplied with a heavy armor, whereas in modern fishes there is a tendency for lighter scales of a different type. The amphibians of the present day are generally smooth and scaleless, but the ancient Amphibia had scales and bony plates. The covering of modern reptiles is either scales or bony plates, though a few smooth forms appeared among ancient reptiles. Birds have scales on their feet and legs, and the feathers of birds are highly specialized structures that appear to have been derived from scales. Hair, the characteristic covering of mammals, is also probably associated with scales in its origin. It serves admirably in preserving a stable temperature and in protecting the body. Scales appear in some mammals, however, being found on the tails of many, on the feet, and often in embryonic development. A small order to which the pangolin belongs consists of animals entirely covered with large epidermal scales, and the group of American edentates, represented by the armadillo, has a covering of bony plates formed from the corium.

Endoskeleton

The greatest advance made by the early chordates was in the development of the internal stiffening rod, the notochord, and the vertebrates have improved on this simple device by forming a complete inner skeleton of cartilage or bone that is far superior to anything to be found in the invertebrates. To support the weight of an animal with an outside skeleton requires an enormous amount of material compared to what is needed in an internal supporting system. No invertebrate living out of the supporting water has been able to reach any great size or weight because they cannot develop a supporting exoskeleton capable of bearing great weight. The largest invertebrates, those found in the Mollusca and the Arthropoda, though quite large, are supported by the water in which they live, and are utterly unable to adapt themselves to life on land. Some of the squids of the present reach a length of forty feet, some of the crustaceans of the past were six feet in length, and the extinct giant dragon flies had a wing spread of two feet; but the limit of size among the invertebrates generally is soon reached, and they can grow no larger. The insects are remarkable mechanically and have a proportionate strength far above vertebrates of the same size, but there is a definite limitation to the weight that they can support with their outside cuticular skeleton.

Skull

The anterior end of the body in all vertebrates is supplied with some form of brain case or skull. The skull originally surrounds only

the brain but early in the history of the vertebrates, it becomes combined with the first two gill arches which give rise to the upper and lower jaws. The skull, which is comparatively simple in the lampreys and hagfishes and somewhat resembles a cartilaginous box in the sharks and their allies, reaches its greatest development in the higher vertebrates.

The cartilaginous type of skull found in the lamprey and the shark was covered with a heavy armor of bony plates in the more primitive forms. In the bony fishes a series of elements is added to those that develop out of the cartilaginous chondrocranium, by the incorporation of the dermal plates, which form a bony covering for the cartilaginous skull. The history of the skull shows how elements found in a primitive structure have been later utilized in many different ways. For instance, in land vertebrates elements associated with the gills of fishes are superfluous and disappear or change in function. The history of the ear and its bony structures reveals a number of interesting cases of change of function, whereby bones used in fishes for support were transformed so as to conduct sound waves to the inner ear.

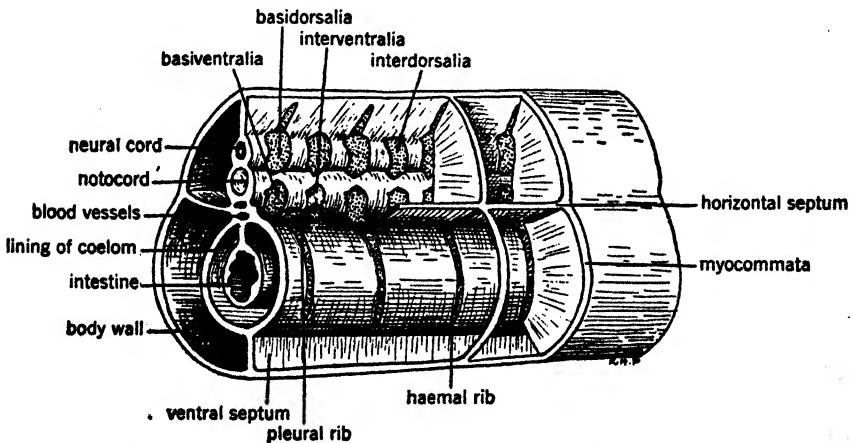


FIG. 5. Diagram of the developing body of a vertebrate, showing the relation of the septa, skeletal parts, and coelom. After Goodrich.

Vertebral Column

The original notochord of the lower chordates undergoes a series of changes in the vertebrates and is finally replaced by the vertebral column, although it still appears in the early developmental stages of every vertebrate (Fig. 5). This series of changes begins when mesodermal tissues are gradually condensed around the notochord, which serves somewhat as a core for them. At first these tissues are small semicircles; later they encircle the notochord as segmental rings, and

eventually they develop into vertebrate. Thus the axial skeleton is changed from a continuous rod to a series of jointed units. The relation of these units to the original segments of the body is such that each completed vertebra lies in two segments, the anterior half in one and the posterior half in the next segment. The vertebra, when fully formed, surrounds the notochord with a band which gradually pinches it out, either by constricting it or by sending spear-like processes into its substance, so that at last the notochord is largely obliterated. The vertebrate become specialized in each region of the body and develop processes that hold them together although still permitting free movement. The ribs and sternum of the animals above the fishes make their appearance with land life; although ribs of two different types are present in the fishes, the sternum is strictly a structure of the higher classes of vertebrates.

Appendages

The appendages of all vertebrates have a characteristic form and arrangement of parts. The limbs of amphibians, reptiles, birds, and mammals are comparable to the paired fins of fishes. The fins, though very variable, have a number of common characteristics, especially in position. On the sides of the body there are typically two pairs of fins, a pectoral pair near the head and a pelvic pair near the anus. Besides these paired fins, fishes have median fins derived from a single median structure that originally extended around the animal both dorsally and ventrally. This original continuous structure was modified by the specialization of the tail and by the elimination of sections, so that separate dorsal and ventral fins were left. Pectoral and pelvic girdles began to develop early in the history of fishes, being attached to the other skeletal structures slightly at first as in the sharks but gradually acquiring a firmer connection. With the development of skeletal supports and the growth of muscles the possibility of movement becomes assured. The limbs of amphibians and higher vertebrates, in contrast to fins, are land structures primarily, and, although probably derived from fins, they are much better organized. Whatever changes may take place in them, the basic plan always remains the same. In land animals the pectoral girdle is firmly imbedded in muscle, while the pelvic girdle forms an attachment to the vertebral column. The paddle-like limbs of aquatic forms of the higher vertebrates retain the structure of a tetrapod limb and not that of a fish fin.

Nervous System

The nervous system of vertebrates (Fig. 2) is based upon centralization, with the brain and the spinal cord as the commanding parts.

(Fig. 4.) It always originates in the same way, by the formation of a neural tube along the back of the embryo. The anterior end of this tube becomes the brain, and the nerve fibers grow out from the sensory ganglia and basal region to supply the sense organs with their necessary sensitive structures and to control the muscles in all parts of the body. As the vertebrate scale is ascended from fishes to mammals, there is more and more centralization in the brain, and with this centralization come added parts, increase in size, and better coordination. Thus the actions of the higher vertebrates become more and more under the control of brain centers, though numerous reflexes remain. The autonomic, or sympathetic, system is perhaps a strictly vertebrate characteristic, as nothing comparable to it is recognizable in the other chordates or in any other animals. It always plays an important part in the organization of the vertebrates.

Sense Organs

Closely associated with the history of the brain are the sense organs, which always are connected with parts of the brain in which their centers are located. Some sense organs exhibit much more variation than others. The nose is always located at the anterior end of the animal and changes with development of land life. The eyes, which differ in type from anything found in the invertebrates, are stable throughout the vertebrate groups and vary little in principle from the lowest to the highest. The ears as organs of equilibrium are constructed on principles similar to those of the otocyst structures of the invertebrates. Their liquid-filled tubes, the semicircular ducts, are supplied with sensory patches in which special cells extend their sensitive parts into the liquid; and any movement of the body causes the endolymph of these tubes to move, so that the calcareous otoliths, or "ear stones," touch the sensitive hairs. The sense of hearing starts with fishes, and is associated with definite sensory patches in the inner ear. The centers of equilibrium associated with the semicircular ducts, and the centers of hearing, are in different parts of the brain. Taste and numerous other senses of lesser importance are common in the vertebrates, but most of these are modifications of the sense of touch and have rather simple anatomical structures.

Digestive System

The digestive system consists essentially of a tube with an inlet, the mouth, and an outlet, the anus. Even in the lowest vertebrates the tube shows some differentiation of its parts, and in the fishes it has a number of distinct regions, always with a stomach and an intestine of one or more parts. In the higher vertebrates, as the body becomes

more specialized, the digestive tube also becomes more complicated, with a strict division of labor in the complicated processes that it has to carry on. Two large glands, the liver and pancreas, are universal in the vertebrates (Figs. 2, 4).

Coelomic Cavity

The coelom, or mesodermal body cavity, becomes divided into two or three cavities in the vertebrates. The first limitation of the coelom is by the development of the septum transversum in the fishes, forming the pericardial cavity, which persists in the higher vertebrates. In mammals there is a further division of the coelom by the development of the muscular diaphragm, which encloses the lungs in two pleural cavities. The remaining cavity, containing the stomach, intestines, liver, kidneys, and other organs, is now called the peritoneal cavity. The coelom is lined with a mesodermic sheet derived from the walls of the hypomere, while folds of this same material form the mesenteries which hold the organs in place and supply the serosa which covers the intestines and other organs. (See Fig. 206.)

Respiration

In contrast to the invertebrates with their varied means of respiration, this function in the vertebrates is localized in one region, the pharynx. They may have tried other regions but only those chordates with the pharyngeal structures modified for the taking of oxygen from the water have survived. The mouth and throat region, being in close contact with the water, could do this with but little modification. The posterior end of the digestive tube was also available and is sometimes used for this purpose. The gills, with their lamellae or filaments, give the greatest exposure to the water, and the gill pouches and slits further increase the efficiency by permitting a steady stream to pass through them. Capillaries bring the blood near to the water in the gills so that exchange of gases is made easy. This is the system used in all fishes and in some amphibians. Any animal entirely dependent on such a system must die when changes in the water destroy the supply of oxygen. The swim bladder, functioning as a lung, permitted some fish to survive under such conditions. The swim bladder, a structure present in early as well as modern fishes, is an outgrowth from the pharynx as a rule. It is used today by the lungfishes and by a few others as an accessory organ of respiration, but in most higher fishes it serves as a hydrostatic organ, regulating buoyancy. In land animals this structure probably became the main breathing organ, or lung, by completing the means of circulation of the blood already started in the fishes. With the advent of lung-breathing the gill slits tended

to close, sometimes remaining open in the amphibians, but always closed in the higher animals which develop special breathing passages through the throat and nose.

Circulation

The circulation of the vertebrates is a closed system, and the haemoglobin is in special cells, the erythrocytes, which are new blood structures not found in the invertebrates. The forcing system is much improved and depends upon a definite muscular heart, which is a modified section of a blood vessel. In the animals above the protochordates the heart always has at least two major chambers, one receives blood and the other sends it to the body. In amphibians it is divided into three chambers; and finally in some reptiles, all birds, and all mammals it has four chambers, two receiving and two forwarding. Valves which prevent any backflow of the blood develop between the heart chambers, and all outgoing vessels from the heart are provided with semilunar valves, as also are the veins in all parts of the body. The blood itself does not diffuse through the tissues of the body but is always confined in arteries, veins, or capillaries. The arteries have fairly thick walls; the veins have walls that are comparatively thin. The capillaries are extremely small and very thin walled, permitting the escape of the plasma and the white corpuscles, so that these may come in direct contact with the cells. The blood vessels, being surrounded by a muscular sheet, are able to decrease or enlarge their caliber under control of the vasomotor nerve connections. The lymphatic system, always in close connection with the rest of the circulatory system, brings back into circulation the fluids that have escaped from the capillaries.

Excretion

Excretion is carried on principally by structures that extract the waste materials gathered up in the circulation around the body. The kidneys, the primary organs in this work, are connected with the circulatory system, and a stream of blood is constantly passing through them. According to their structure and phylogeny, the kidneys fall into three types in the chordates: (1) the pronephros, the primitive kidney, loosely organized and found only in the lowest vertebrates and in embryonic development of other vertebrates; (2) the mesonephros, the kidney of the fishes and amphibians, which is much larger and much more effective in its work, because of its better mechanical arrangement and its improved and more numerous units of structure; and (3) the metanephros, the kidney of the reptiles, birds, and mammals, which is more compact and by its structure better suited for its

function. The blood supply of the kidneys comes primarily from the arterial system, partially so in fishes and amphibians, and entirely so in birds and mammals, with the reptiles transitional. With each complete circuit of the blood around the body, a portion is led by arteries and capillaries into the structural units of the kidneys, and portions of the water, urea, uric acid, salts, and other wastes are able to get through the separating membranes of Bowman's capsule and into the tubules. The tubules are lined with cells which make a selection of the materials exposed to their walls, and thus return to the blood a part of the water and materials that are not waste. The renal portal system, typical of fishes and amphibians, conducts the venous blood from the posterior end of the body, winds around the tubules of the kidney units, and exposes the blood to these active cells. A urinary bladder may or may not be present (Fig. 4).

Reproduction

Starting with the fishes, the vertebrates normally have separate sexes. The young are developed from fertilized eggs, which may be laid or may be retained in the body until hatched, or may be attached to the wall of the uterus by a placenta as in the highest mammals. The placenta serves as a structure through which food is conducted through membranes, waste is returned to the mother for excretion, carbon dioxide is removed, and oxygen supplied. The genital organs and kidneys have parts in common, especially in the males of the higher vertebrates, where the same ducts may carry the products of both. Fertilization is generally external in water-dwelling vertebrates, and internal in the animals that are terrestrial.

The Problem of the Ancestry of the Chordates

The chordates appeared comparatively late in the history of animal life. It seems probable that they were derived from a line of ancestry that extended far back in the geological periods, in fact back to the time of the origin of most of the invertebrate phyla. Most of the evidence of their ancestry has been lost, since the early chordates were soft bodied, so that preservation of the critical parts was unlikely. Many theories have been proposed concerning the possible ancestral lines; but, since all the evidence so far is circumstantial, no one theory has been entirely satisfactory.

One of the earliest theories was that of Geoffroy St.-Hilaire (1807), who evidently spent a great deal of time speculating on the relationships of different animals and trying to make them all fit a common mold. His ideas are rather remarkable, since they came at a time

long before any definite concept of evolution was formulated. He had made the discovery that the skulls of young animals were much better than those of old ones for the study of the separate elements of which they were composed, and he used them in making his comparisons. He decided that dorsal and ventral meant little, and to support this he cited animals that had changed their orientation, such as the back-swimming insects (*Notonecta*), the squids, and the flat fishes such as the halibut. He compared the chitinous rings of insects to vertebrae, compared the position of the viscera and exoskeleton of insects to the conditions found in the turtle with its shell, and considered that the legs of insects could be compared to the ribs of vertebrates. With the belief that all animals could be fitted to a common pattern, he conceived the idea that the insect, if turned on its back, could be made to agree with the conditions found in the vertebrates as he knew them then. Although this theory is interesting, it adds nothing to our knowledge of the origin of the chordates.

Nemertean Theory

The nemertean worms were suggested by Hubrecht (1883) as possible ancestors of the early chordates. He assumed that the proboscis sheath could be compared to the notochord and that cephalic pits could be compared to gill slits. The lateral paired nerve cords, he thought, could have migrated dorsally to form a single cord comparable to the central nervous system, leaving a pair of lateral nerves that would correspond to the lateral branches of the vagus nerve of the chordates. Though of some interest, this theory has received little attention, since there are few facts on which to base any such assumptions.

Arachnid Theory

Patten, in his numerous papers, and in his books, the "Evolution of the Vertebrates and Their Kin" (1912) and "The Grand Strategy of Evolution" (1920), presents a very ingenious theory to account for the origin of the chordates. He ignores the protochordates entirely as specialized offshoots that lead nowhere. He maintains that *Amphioxus*, the tunicates, and *Saccoglossus* with its echinoderm affinities were derived from an early invertebrate phylum and have no place in the phylogeny of the vertebrates. His ancestral line of the chordates is through the primitive arachnids such as *Limulus*, the primitive arthropod *Eurypterus*, and thence through the ostracoderms to the fishes. In comparing the arachnids and the chordates he finds many points of similarity in the brain, heart, and aortic arches, and in the presence of gill pouches and external gills. Although many of the similarities

are striking, there is the possibility that convergence and coincidence should receive more consideration. He states that the different parts fit together like a picture puzzle, and if one follows his writings and illustrations it certainly appears to be so. Although interesting this theory does not have wide acceptance.

Arthropod Theory

The most fantastic theory is that of Gaskell (1896), who attempts to derive the chordates from the arthropods by a series of structural and functional changes that are startling in their boldness. From his studies on arthropods and cyclostomes, he has come to the conclusion that the old digestive system of the arthropod became surrounded with nerve tissue and gave rise to the brain and spinal cord, and that the ancestral mouth is represented by the infundibulum of the chordate brain. He supposes that a new digestive system was formed from the ventral wall of the body by a similar process. Such alterations of function seem absurd, and to assume that they occurred does not make our problem any less difficult.

Annelid Theory

The annelids have been a favorite group in the search for chordate ancestry, and after the publication of Darwin's "Origin of Species" they were studied intensively by numerous workers: Dohrn, Semper, Delsman, and others. The attention of these students of phylogeny was attracted to the annelids because of several features that seemed to be comparable to chordate characteristics, such as the segmentation of the body, the repetition of the urinary tubules (a condition discovered in the shark at about this time), the presence of a coelom, red blood, lateral locomotive organs, and a concentrated series of segments suggesting a head. It is now known that segmentation has occurred in numerous phyla and that it is not a fundamental character. The annelids offer no good evidence for the origin of gill slits, and although a structure called the "Faserstrang" has been compared to the notochord it is considered rather questionable. The "Faserstrang" is a string of cells that underlie the nerve cord and is enclosed with it in a common sheath. The embryological development is entirely different from that of the chordates. The annelid theory leaves too much to be explained and has little support today.

Amphioxus Theory

The *Amphioxus* theory of Willey and others considers the proto-chordates as being in the line of evolution between the vertebrates and the hypothetical invertebrate phylum from which they branched off.

Wiley stresses the importance of the three fundamental characters of the chordates as found in *Amphioxus* and traces their ancestry to some worm-like form that was perhaps associated with the bilateral ancestors of the echinoderms. Thus the urochordates would be modified chordates related to *Amphioxus*, and *Saccoglossus* of the hemichordates would be a representative between the chordates and the echinoderms. Wiley in his "Amphioxus and the Ancestry of the Vertebrates," says: "For the present we may conclude that the proximate ancestor of the vertebrates was a free-swimming animal intermediate in organization between the ascidian tadpole and *Amphioxus*, possessing the dorsal mouth, hypophysis, and restricted notochord of the former, and the myotomes, coelomic epithelium, and straight alimentary canal of the latter. The ultimate or primordial ancestor of the vertebrates would, on the contrary, be a worm-like animal whose organization was approximately on a level with that of the bilateral ancestors of the echinoderms."

This theory would only carry the vertebrate back to a prevertebrate ancestor and would not solve the ancestry of the chordates. Lately the tendency has been to consider *Amphioxus* a highly specialized and perhaps degenerate modern form and to consider that the ammocoetes or larval lamprey more closely resemble the hypothetical ancestral prevertebrate.

Echinoderm Theory

One of the more recent theories of the origin of the chordates is that they arose from the same stock as the echinoderms. The evidence of relationship rests principally on the similarity of the larvae of the hemichordates (*Saccoglossus*) and the larvae of some of the echinoderms. The embryological development of both groups shows close similarity. Both have indeterminate cleavage and the same mode for the formation of the coelomic pouches, and both have the anus formed from the blastopore. Biochemical tests (Needham *et al.*, 1932) and serological tests (Wilhelmi, 1942) have indicated a closer relationship of the echinoderms to the chordates than to any of the non-chordate phyla. There is a close resemblance between some of the Paleozoic echinoderms with tendencies toward bilateral symmetry and some of the primitive ostracoderms.

The hemichordates are not in good standing as chordates but they are probably descendants of an early offshoot of the stem from which chordates arose. Although the adults of modern echinoderms and chordates differ most widely in structure, the structure of the primitive ancestors before these modern phyla were established could easily have been alike. The similarity of several fundamental characters

and their embryological development point toward a common ancestry. This theory offers more possibilities than any of the others and is better supported by fundamental evidence. Consequently it is the most widely accepted theory of the origin of the vertebrates.

The ancestry of the chordates will probably never be solved beyond doubt and will always remain hypothetical as these stem forms may have been soft bodied and left no fossil remains to prove definitely the ancestral type. The original stem arose before most of the phyla, as we recognize them, were differentiated. Similarity of structures between the chordates and other existing phyla are probably often cases of parallelism. The modern forms constituting present phyla have become so highly modified and so greatly changed from their ancestral stems that attempts to relate them involve many hazards.

CHAPTER TWO

Classification

Animals are classified for convenience, and their apparently formidable scientific names are really stenographic terms that save time and avoid confusion in identifying groups and species. Common names differ and may have only local currency, but the use of technical names makes it possible for scientific workers in all parts of the world to communicate their results. Before the days of the binomial system, a lengthy list of descriptive words was used, together with a common name, for designating a kind of animal, but of course this was so cumbersome and unsatisfactory that it could not readily be used in any scientific way. John Ray (1627-1705) is given the credit for having invented the binomial system of designation, and to the great Swedish scientist Linnaeus should go the credit for making such good use of the system in his "Systema Naturae." By this system an animal has two names, a generic and a specific; for example, *Homo sapiens* is the scientific name for man. For subdivisions, a third name may be applied, giving a distinction of varieties.

The history of classification shows the growth of the study of animals, since the early classifications, such as Aristotle's, were founded on a study of a small number of animals in a restricted region, whereas a modern classification includes the animals of the world, not only of the present but also of the past. Modifications have been necessary from time to time, as new animals were found. When *Ornithorhynchus*, Fig. 37, *Archaeopteryx*, Fig. 33, *Hesperornis*, Fig. 34, *Moa*, *Pithecanthropus*, *Amphioxus*, Fig. 7, and other striking forms were discovered, radical changes were made in classification, with additions of groups to include these different forms.

The long series of names used for the major and minor divisions of the vertebrates, as shown in the accompanying table, are merely convenient ways of indicating a number of forms united by a common set of characters. The characters of each group, though fixed arbitrarily, are supposed to express phylogenetic relationships. Any of these terms may be modified by a prefix, super- or sub-, to make them include more or less. The following list, beginning with the major division

(phylum) of the animal kingdom and showing the following subdivisions in sequence, includes most of the terms now used in chordate classification:

Phylum	Chordata
Subphylum	Vertebrata
Superclass	Tetrapoda
Class	Mammalia
Subclass	Eutheria
Order	Carnivora
Suborder	Fissipedia
Family	Canidae
Genus	<i>Canis</i>
Species	<i>domesticus</i>
Subspecies	<i>albinus</i>

Probably the first classification was made by primitive man when he differentiated animals into those that were suitable to eat and those that were not. The ancient hunters divided animals into those found on land and those found in or around water. Some early attempts at scientific classifications were on this ground, but proved unsatisfactory because they did not differentiate the fishes from the amphibians, the aquatic mammals, or other groups that make their homes in water. For many centuries the whale was called a fish. Aristotle used egg-laying as a means of separating animals, and, though not a good measuring stick, it served very well for the time. Linnaeus took over most of the work of Aristotle without change, and thus continued this classification. John Ray used the blood as a means of separating the animals; and, since he had a much greater knowledge of anatomy at his command, he was able to work out some very significant improvements on the work of those who preceded him. Richard Owen based his classification on the form of the brain. The great impetus given to classification by Darwin's "Origin of Species" (1859) completely changed the trend, and from then to the present time classification has had a very different meaning. Instead of few external characters, the whole animal is now used, and with a greater knowledge of anatomy the grouping has been placed on a much sounder basis. Superficial resemblances and convergent forms have been separated and have been placed more nearly in their proper relationships. With evolution and phylogeny as central ideas, the study of classification has been assisted by many phases of zoölogy, such as anatomy, embryology, paleontology, geographical distribution, and, in more modern times, physiology and genetics—each of which has contributed to make the lines of differentiation more

exact. Classification probably will never be fixed or static but must change with additional knowledge that makes more certain the relationships of animals, both those now living and those that are extinct. This fluidity of classification is well illustrated by a consideration of the changes that have occurred in the classification of fishes from the time of Linnaeus to the present. The older conception of a single class has been expanded until there are now four or more well-defined groups raised to the importance of classes.

The following classification will give a general outline of the arrangement of the chordate groups with a brief summary of the characters of each division and subdivision.

Summary of Characters of the Groups and Subdivisions of the Chordata

PHYLUM CHORDATA. Bilaterally symmetrical; notochord and pharyngeal gill slits present at some stage of development; nervous system dorsal to the digestive tube.

- A. Subphylum **Urochordata.** Adults quite different from larvae; body of sessile forms enclosed in cellulose mantle; gill slits and endostyle present in pharynx; a heart; sense organs in larvae. Examples: (Fig. 6) *Tunicata*, *Salpa*, *Appendicularia*.
- B. Subphylum **Cephalochordata.** Small lancet-shaped animals living along the seashore. Head not well defined; notochord extends from tip of nose to tail; heart one-chambered and tubular; no paired appendages; no cranium; no blood corpuscles; gills in peribranchial chamber; epidermis one cell in thickness. Examples: (Fig. 7). *Amphioxus* (*Branchiostoma*).
- C. Subphylum **Vertebrata.** Definite head, skull, and sense organs; red blood, circulation a closed system; heart of at least two cham-



FIG. 6. A urochordate.

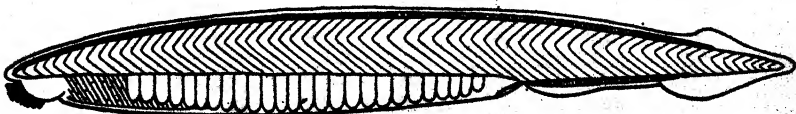


FIG. 7. *Amphioxus*.

bers; brain complex and divided into definite regions; nephridial tubes usually carrying away sex products; notochord reaching only to the ear region; vertebral column in some stage of development; few with larval development.

TABLE SHOWING CLASSIFICATION OF PHYLUM CHORDATA

Extinct groups are indicated by the asterisk (*)

- A. Subphylum Urochordata.
- B. Subphylum Cephalochordata.
- C. Subphylum Vertebrata.
 - 1. Superclass Pisces.
 - a. Class Agnatha.
 - Order Osteostraci.*
 - Order Anaspida.*
 - Order Heterostraci.*
 - Order Cyclostomata.
 - b. Class Placodermi.*
 - c. Class Chondrichthyes.
 - Subclass Elasmobranchii.
 - Subclass Holocephali.
 - d. Class Osteichthyes.
 - Subclass Actinopterygii.
 - Superorder Chondrostei.
 - Superorder Holostei.
 - Superorder Teleostei.
 - Subclass Choanichthyes.
 - Superorder Crossopterygii.
 - Superorder Dipnoi.
 - 2. Superclass Tetrapoda.
 - a. Class Amphibia.
 - Subclass Apsidospondyli.
 - Superorder Labyrinthodontia.*
 - Superorder Salientia (Anura).
 - Subclass Lepospondyli.
 - Order Aistopoda.*
 - Order Neotridia.*
 - Order Microsauria.*
 - Order Urodela.
 - Order Apoda (Gymnophiona).
 - b. Class Reptilia.
 - Subclass Anapsida.
 - Order Cotylosauria.*
 - Order Chelonia (Testudinata).
 - Subclass Ichthyopterygia.
 - Order Ichthyosauria.*
 - Subclass Synapsosauria.
 - Order Protosauria.*
 - Order Saurpterygia.*
 - Subclass Lepidosauria.
 - Order Eosuchia.*
 - Order Rhynchocephalia.
 - Order Squamata.
 - Subclass Archosauria.
 - Order Thecodontia.*
 - Order Crocodilia.
 - Order Pterosauria.*
 - Order Saurischia.*
 - Order Ornithischia.*
 - Subclass Synapsida.
 - Order Pelycosauria.*
 - Order Therapsida.*
 - Order Ictidosauria.*
 - c. Class Aves.
 - 1. Subclass Archaeornithes.*
 - 2. Subclass Neornithes.
 - (a) Superorder Odontognathae.*
 - (b) Superorder Palaeognathae.
 - d. Class Mammalia.
 - 1. Subclass Prototheria.
 - Order Monotremata.
 - 2. Subclass Metatheria.
 - i. Order Marsupialia.
 - a. Suborder Polyprotodontia.
 - b. Suborder Caenolestoidae.
 - 3. Subclass Eutheria.
 - i. Order Insectivora.
 - ii. Order Chiroptera.
 - iii. Order Dermoptera.
 - iv. Order Pholidota.
 - v. Order Xenarthra.
 - vi. Order Lagomorpha.
 - vii. Order Rodentia.
 - a. Suborder Simplicidentata.
 - b. Suborder Duplicidentata.
 - viii. Order Carnivora.
 - a. Suborder Fissipedia.
 - b. Suborder Pinnipedia.
 - ix. Order Cetacea.
 - x. Order Hyracoidea.
 - xi. Order Proboscidea.
 - xii. Order Sirenia.
 - xiii. Order Artiodactyla.
 - xiv. Order Perissodactyla.
 - xv. Order Tubulidentata.
 - xvi. Order Primates.
 - a. Suborder Lemuroidea.
 - b. Suborder Tarsioidae.
 - c. Suborder Anthropoidea.

Orders of extinct mammals are omitted as the status of some is not clear and they are seldom referred to in elementary comparative anatomy.

The accompanying classification adapted from that of Romer (1945) and other recent writers, divides the vertebrates into two main groups on the basis of their mode of life, i.e., the Pisces or water vertebrates and the Tetrapoda or land vertebrates. Other workers have divided the vertebrates on the basis of jaws, placing the earliest jawless vertebrates in the Agnatha and all the other vertebrates in the Gnathostoma or forms with jaws. Only the most primitive vertebrates are without upper and lower jaws and are represented by the earliest fossil fish-like forms and the living cyclostomes.

All the higher vertebrates including our living fishes possess upper and lower jaws. The development of these jaws was one of the important steps in the early stage of vertebrate evolution. It enlarged enormously the choice of foods, in comparison with that possible to animals with sucking, jawless mouths, and allowed the vertebrates to follow endless lines of specialization. The origin of jaws came with a change in the function of the anterior supporting structure of the first gill and was an important event in the evolution of the vertebrates, separating the vertebrates into two widely differentiated groups. In the same way, the change from water life to land life was another great shift which was accomplished only by great changes in structures. Structures for respiration, locomotion, and many other purposes underwent radical changes. The structural changes involved in this transition from water to land also readily separate the vertebrates into two major divisions: the Pisces or fish-like vertebrates and the Tetrapoda or four-footed vertebrates.

Diagram 1 arranges the various groups of vertebrates to show their probable origins or phylogenetic relationships.

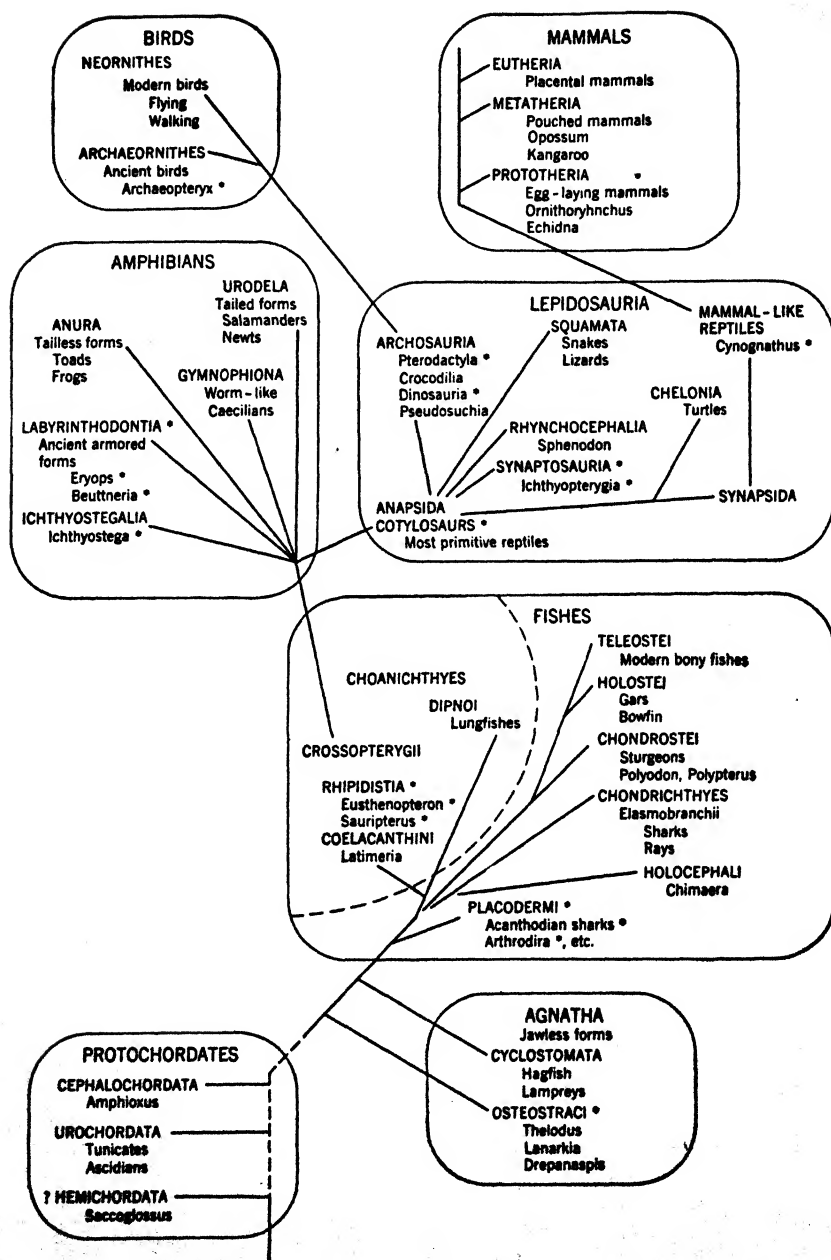


DIAGRAM 1. The phylogenetic relationships of the chordate groups.
Fossil forms are indicated by the asterisk (*).

CHAPTER THREE

Superclass Pisces or Fish-like Vertebrates

The vertebrates may be divided into the fish-like vertebrates, the Pisces, and the four-footed land vertebrates, the Tetrapoda. The Pisces were at one time considered one class equivalent to the Amphibia, Reptilia, Aves, or Mammalia. The differences between the various groups of the fish-like vertebrates are so great, however, that they may be divided into a number of classes. Studies of the anatomy of both living and many recently discovered fossil forms have shown us that the fish-like vertebrates can be divided into the classes Agnatha, Placodermi, Chondrichthyes, and Osteichthyes.

We study fishes, not only for their own sake, but also because they possess almost all the structural elements from which the characteristic structures of higher vertebrates have developed. Though living in water, fishes have the essential parts that provide a foundation for the growth of organs needed on land. Thus the limbs of tetrapods originated from fins, lungs from swim bladders or from gill pouches, jaws from gill arches, teeth from scales, and feathers and hair from epidermal appendages, probably scales. It is necessary to go far back into the geological ages to get the starting point in the history of fishes. The earliest true fishes appeared in the Devonian and possibly in the Silurian period (p. 34), and to discover the first fish-like forms would require exploration of even earlier periods. Their primitive ancestors were probably soft bodied, with no hard parts that were preserved in the rocks; for this reason their traces are difficult to identify. Starting with known conditions as found in the ostracoderms and cyclostomes, we can infer what equipment the primitive forms possessed. From protochordate ancestors they inherited a segmented body with well-developed muscle segments, the myotomes, and their separating sheets of connective tissue, the myocommata, that enabled them to move about on the bottom and gradually assume an active water life. From these early undulating movements fishes developed their characteristic types of locomotion and organization. A definite body shape came with continued movement in a forward direction, and even the earliest forms must have had well-differentiated anterior and posterior ends.

The anterior end became specialized as the entrance to the digestive tube with its sensory accessories, and the posterior end became modified and specialized for locomotion. The ancestral fish probably resembled somewhat the larval ammocoetes of a cyclostome or *Amphioxus*, possibly a combination of both. It is possible that the earliest fishes retained a ciliary ingestion and got their food through a primitive sucking mouth, aided by a ciliary tract that conducted the food particles into the gullet. Very early in the history of fishes a new type of mouth was developed, using the opening of the gills and a part of their skeletal support for the formation of grasping or biting jaws. The sense of smell had been developed early, and now the eyes became an aid in food-getting. A sac-like ear, possibly formed from the lateral line, gave the required sense of balance. Fins as such came after a long period of time, and it is quite probable that they followed the development of the finfold or else had an independent origin. (See chapter on skeleton.)

Class Agnatha

The Agnatha are vertebrates which possess jawless, sucking mouths and are without well-developed paired appendages. The brain is rather primitive. The only living forms are the lampreys and hagfishes of the order Cyclostomata. These are highly specialized modern forms, and, although they retain some primitive characters, they have probably lost many of their ancestral characters. Three extinct orders generally known as the ostracoderms are the Osteostraci, the Anaspida, and the Heterostraci. These have an armor of heavy plates which contain some bone. We know little about their internal skeleton.

In the last fifty years the ostracoderms (see Fig. 8) have shifted from a position of incertae sedis to a place of real importance in the vertebrate series. For years so little was known of them that they were illustrated with the dorsal side oriented downward. With perhaps the exception of Otto Jaekel's "Die Wirbeltiere" in 1911, this misinterpretation was true of all the illustrations of *Birkenia* and *Lasanius* published before 1920. The cause of the misinterpretation was probably the poor preservation of the available specimens. Later the discovery of a rich bed of finely preserved specimens in Spitzbergen gave an opportunity to secure better specimens. Through the work of Stensiö, Kiaer, and others, the group gradually took shape and became much better defined. Many of these Spitzbergen specimens were of such a high quality that sections could be made through the head and other regions. Thus the outline of the brain, the spinal nerves and blood vessels, and the foramina or openings in the skull, could be determined with accuracy. It was found that there were a number of characters

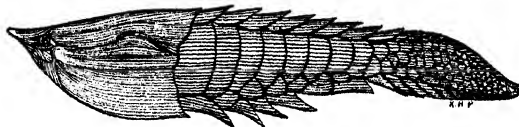
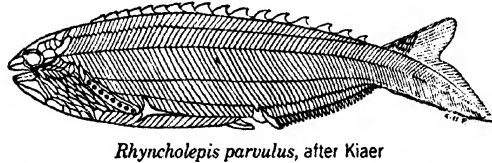
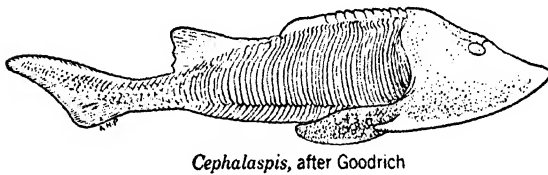
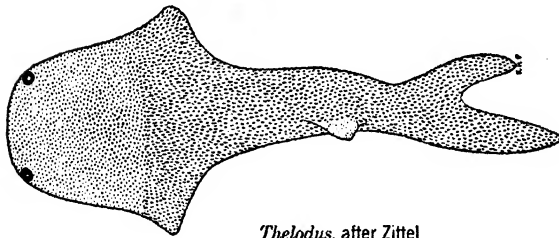
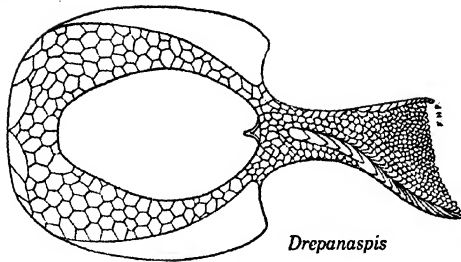


FIG. 8. Class Agnatha, ostracoderms.

that connected the ostracoderms with the cyclostomes, including the jawless mouth, a similar type of brain and spinal nerves, two semi-circular ducts in the ear, and the nature and structure of the gill pouches.

The ostracoderms appeared in the Ordovician period (p. 34) and

died out in the Devonian, leaving no descendants, except possibly the cyclostomes, which some consider a modern offshoot. These animals were generally small, usually only a few inches in length, the largest reaching a length between one and two feet. The presence of bone in their covering plates, scales, and skulls places the appearance of bone very early in vertebrate history. Their remains are found all over the world, but the main beds are in England, Norway, and on the Island of Oesel in the Baltic.

Order Cyclostomata

The cyclostomes (Fig. 9) are eel-like animals, members of an ancient fauna existing from the time of the ostracoderms of the Silurian and other early geological periods. Nothing is known of their paleontological history, since their bodies are soft and fossilization a matter

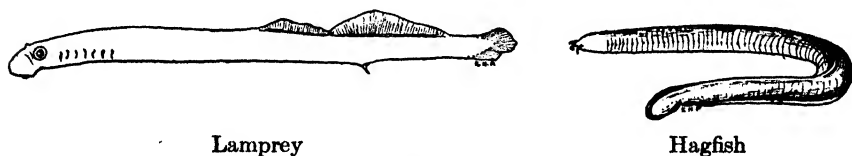


FIG. 9.

of chance. The work of Stensiö and others has shown that the ostracoderms and the cyclostomes have much in common, and their relationship is now well established and generally accepted. Long before this relationship was known, the cyclostomes had been recognized as an ancient group that had persisted from the early days of chordate life, they have a number of truly primitive characteristics.

The cyclostomes have a world-wide distribution and live in both fresh and salt water. The number of genera and species is comparatively small, although the number of individuals is relatively large. The cyclostomes fall into two well-marked divisions, the suborder Myxinoidea or hagfishes (Fig. 9) and the suborder Petromyzontia or lampreys (Fig. 9). All the Myxinoidea are salt-water forms, whereas the Petromyzontia live in both fresh and salt water. The Myxinoidea burrow into fishes and devour them alive; some are hermaphroditic. The Petromyzontia are mostly parasitic blood suckers, but a few have lost their parasitic habits and do not feed as adults. The cyclostomes are placed at the foot of the vertebrate scale (see Diagram 1) because of a number of primitive characters, such as a lack of jaws; a single median nostril; only one or two semicircular ducts in the ear; lack of denticles or scales; lack of paired fins; a primitive condition of the vertebral column, in which the notochord may or

may not be covered by incipient neural arches; a membranous condition of the skull roof. There are from six to fourteen pairs of gill pouches which may open to the outside through a single pair of ducts as in *Myxine*, or each gill may have an opening as in *Bdellostoma* and in the *Petromyzontia*.

Suborder Myxinoidea (Hagfishes)

The Myxinoidea (Fig. 9) have a single, terminal nostril; the dorsal fin small or missing but not divided if present; a large, single epidermal tooth; a single semicircular duct in the ear; some are hermaphroditic; gills vary in number from six to fourteen pairs; eyes are vestigial. Some hagfishes bore into the body of fishes and remain in the body cavity until they have stripped the carcass of flesh. They may reach a length of thirty-six inches. The eggs are quite large, twenty-two millimeters long, and are covered with a horny shell.

Suborder Petromyzontia (Lampreys)

Lampreys (Fig. 9) live in both fresh and salt water, but all come to fresh water to lay their eggs. They vary in their habits, some being free living, whereas others attach themselves to fishes and other water animals. They differ from the Myxinoidea in having the single nostril placed between the eyes; have traces of a lateral line system; two semicircular ducts; well-developed eyes; an intricate branchial basket supporting the gills; mouth surrounded by a sucking disc with a battery of small cornified papillae serving as teeth; seven pairs of gill openings. Although some lampreys attach themselves to water animals, they do not bore into the body cavity. Fish in lamprey-infested waters often show scars caused by the sucking disc of the lampreys. The eggs are small, about 0.5 millimeter. The larval young, called ammocoetes, undergo a distinct metamorphosis before attaining the characters of the adults. Some adults of the salt-water species reach a length of thirty-six inches.

The fresh-water lampreys have quite a wide distribution over the United States and are often taken by fishermen as they remain attached to the bodies of fishes when fish are taken into the boats. The young, because of their burrowing habits during the larval stage, often remain unobserved. The eggs are laid in pebble nests, built by the adults, and the young develop and spend their time in the sand and mud in the bottoms of streams. Their food is the microscopic animal and vegetable life that is abundant where they live. The larvae remain in this stage for a number of years, probably from three to seven, when metamorphosis takes place and they attain adulthood. The young differ from the adults in a number of features, among which might be mentioned: a mouth with a well-developed oral hood; a velum separating the mouth from the pharynx; lack of a sucking disc and epidermal teeth; a ciliated groove, often compared with the endostyle of *Amphioxus*, which extends back along the floor of the pharynx; eyes showing as pigment spots; median fin continuous and not lobed as in the adult; otic vesicle large but with parts not well differentiated.

Structure of the Lamprey (*Entosphenus tridentatus*)

The following summary of the anatomy of the lamprey (*Entosphenus tridentatus*) gives the general structure of a typical cyclostome although other

species may vary in some respects. The skin of the lamprey is smooth and slimy, the slime being supplied by an abundance of unicellular glands. There is no indication of scales or plates in any stage of the development.

No paired fins are present in the cyclostomes. There is a rounded fin at about the middle of the back; a second fin starts on the back at about the position of the anus, then extends around the tail, and ends at the anus. The mouth (Fig. 10) is sucker-like and is used at times to attach the lamprey to animals or to stones. It contains a number of epidermal teeth and a rasping tongue, also supplied with horny teeth, which help in rasping a hole in the skin of fishes. The buccal funnel functions as a sucker, with the tongue used

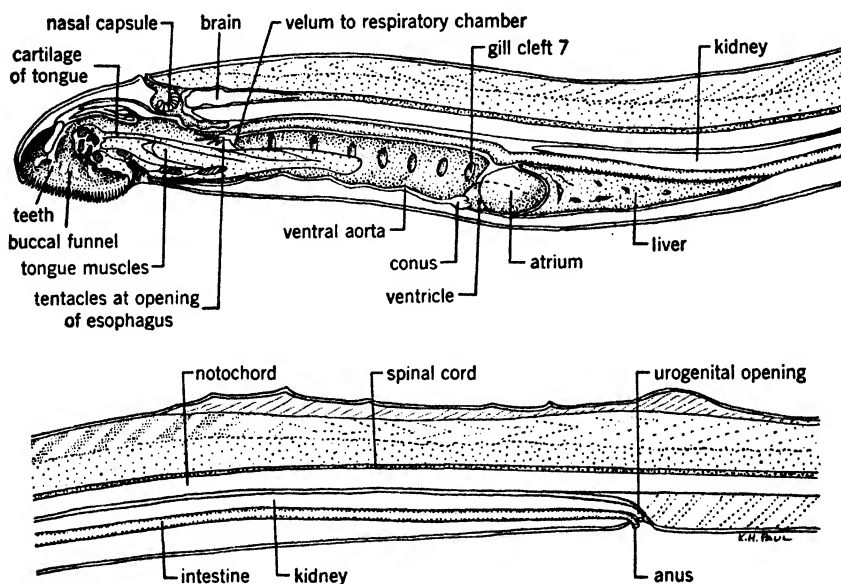


FIG. 10. Sagittal section of cyclostome showing the relations of the organs.

as a plunger to create suction. This highly developed tongue is quite complex and has a long cartilage which anchors it to the body. An effective musculature enables the tongue to move backward and forward and to be used both as a rasping organ and as a plunger. The gill openings are along the side of the pharyngeal region and lead to a respiratory chamber.

The tail is rather blunt with the notochord extending to the tip and with a dorsal and ventral fin.

The skull is very primitive, consisting of cartilaginous structures, the parachordals and trabeculae, which form a trough along the base; the dorsal side of the trough has a membranous roof. The olfactory apparatus is supported by a plate on which the olfactory sac rests. The nasal capsule is median and single. The eye is supported by a subocular arch that serves as a base for these structures. The auditory capsules are attached to the posterior region of the skull.

The main feature of the axial skeleton is the conspicuous notochord, which is not constricted. It is covered with a fibrous and elastic sheath. The Petromy-

zontia have incipient bars of cartilage over the spinal cord, that correspond to neural arches but have no centra. The fins are supported by numerous small rays. There is no trace of any skeletal parts related to either limbs or girdles.

The skeleton supporting the gills consists of a cartilaginous branchial basket of nine bars that have a very complex pattern. The bars are joined to each other, and it is rather difficult to compare them with the gill skeleton or branchial arches of higher vertebrates.

The gills of the Petromyzontia are distinctive, since they are not connected directly with the pharynx, but with a respiratory tube that lies just ventral to the esophagus. The opening to the respiratory chamber is controlled by a strong flap or velum. The gill chambers are lozenge shaped and lined inside with the typical gill filaments. A tube connects each gill to its opening on the outside of the body. Water is taken through the mouth, but the mouth opening is rather small. When the animal is attached, the water system changes and the respiratory chamber, closed by the velum, forces the water in and out through the gill openings. A hydro-sinus on the dorsal side of the mouth cavity is supplied with muscles, and thus the water is forced through the gills and cleans the gills of debris that might accumulate in the tubes.

The digestive tube (Figs. 2, 10) is rather simple, consisting of a small esophagus, a stomach region not differentiated in size, and a small intestine supplied with a typhosole which is a small flap extending along the intestinal floor simulating a spiral valve. The digestive tube extends to the left of the heart, then swings back, taking a mesial position between the kidneys, and extends straight to the anus. The large kidneys and gonads crowd it into the ventral part of the body cavity. At the entrance of the esophagus, a little group of tentacles, directed anteriorly, regulates the flow of food particles into the digestive tube. The food of the parasitic lampreys is in a highly concentrated form, consisting of blood, lymph, body fluids, and rasped bits of flesh. The liver is a large, wedge-shaped, bilobed organ, just posterior to the heart. A large portal vein carries blood from the intestine to the liver, and a hepatic vein returns the blood to the heart. The pancreas is limited to some follicles on the side of the liver. No spleen is present. Some have gall bladders, but *Entosphenus* appears to have none.

The paired kidneys extend the length of the body cavity, starting just posterior to the heart and ending at the anus. There is no renal portal system, and the blood is supplied through segmental arteries. A long urinary duct is located on the ventral side of each kidney, and the urine is conducted to two pores which empty into a urogenital sinus. There is a large blood-sinus dorsal to the kidneys, and between the kidneys lies the single gonad. The eggs and spermatozoa escape into the body cavity and thence through abdominal pores to the outside of the body. Fertilization takes place in water. All the lampreys, both fresh- and salt-water forms seek fresh water for spawning. They enter the streams and ascend to the spawning beds, which are usually in swift water. The fresh-water *Ichthyomyzon unicuspis* lays over 150,000 eggs, and the sea lampreys lay more than 200,000.

The circulatory system of the lamprey, although somewhat more primitive than that of the sharks, is more advanced than the type present in *Amphioxus*. The heart, surrounded by a tough membrane, the pericardium, consists of a large atrium on the left side of the pericardial cavity, a heavy-walled ventricle, and a small conus at the base of the ventral aorta. The collecting veins

THE GEOLOGICAL TIME SCALE

(Modified from Reeds and Lull.)

Psychozoic	Recent	*	Rise of man	AGE OF MAN
Cenozoic	Pleistocene	1	Extinction of great mammals	AGE OF MAMMALS
	Pliocene	7	Origin of man	
	Miocene	19	Culmination of mammals	
	Oligocene	35	Rise of higher mammals	
	Eocene	55	Disappearance of archaic mammals	
	Paleocene	60	Archaic mammals	
Mesozoic	Cretaceous	65	Highly specialized reptiles	AGE OF REPTILES
	Jurassic	35	First birds	
	Triassic	35	First mammals Rise of dinosaurs	
Paleozoic	Permian	25	Mammal-like reptiles	AGE OF AMPHIBIANS
	Pennsylvanian	35	Rise of primitive reptiles	
	Mississippian	50	Fishes and amphibians	
	Devonian	50	Rise of amphibians Rise of bony fishes and ancient sharks	AGE OF FISHES
	Silurian	40	Placoderms	
	Ordovician	85	Rise of armored fishes	AGE OF HIGHER INVERTEBRATES
	Cambrian	70	No fishes known	
Proterozoic		650	Primitive invertebrates	
Archeozoic		650	Unicellulars	

* The figures in this column refer to estimates of the duration of these time periods, in millions of years.

form a sizable sinus venosus on the dorsal side of the heart and empty into the atrium. The ventral aorta extends anteriorly, ventral to the respiratory chamber, giving off vessels (afferent) to the gills. Vessels (efferent) collect the blood from the gills and form a single dorsal aorta, which extends the length of the body, just ventral to the notochord. A large intestinal artery supplies the organs of the body cavity. Anterior to the heart, the venous system consists of a pair of ventral jugular veins and a pair of cardinal veins with the usual branches draining the head region. Posterior to the heart, a pair of posterior cardinal veins carry the blood to the sinus venosus. These lie lateral to the notochord. A portal vein leads the blood to the liver, and an hepatic vein conducts it to the sinus venosus. The blood is red as it has nucleated red corpuscles or erythrocytes. No renal portal system is present; the caudal vein empties directly into the postcardinals.

The brain of *Entosphenus* is typical of the lampreys. It is rather simple in organization but has the same divisions and lobes as in the sharks. The cerebral hemispheres are small and in close association with the rather large olfactory lobes. The diencephalon has two dorsal outpouchings, an interior parietal and a posterior pineal or epiphysis. The anterior outpouching develops a parietal eye. On the ventral side of the diencephalon is a well-developed infundibulum. The midbrain has two well-developed optic lobes, and the cerebellum is represented by a slight band of nerve tissue just posterior to the optic lobes. The myelencephalon, with its fourth ventricle, continues into the spinal cord, which is much flattened. There are ten cranial nerves, the last two being outside of the skull. The spinal nerves are peculiar in that the dorsal and ventral roots come out alternately and do not join.

The peculiar single nostril opens between the eyes, and the nasal passage leads posteriorly to a large and somewhat complicated olfactory sac (Fig. 10). A canal continues posteriorly from this sac to a blind chamber called the pituitary sac lying just anterior to the pituitary structure. The eyes are fairly well developed but are without lids, the whole eye being covered with a transparent skin. A vestigial parietal eye is present but is deeply buried and non-functional. The auditory sac is enclosed in a capsule of cartilage and has only two semicircular ducts, the posterior and anterior. Some parts of the lateral line are represented in the head region.

The ammocoetes has a subpharyngeal gland on the floor of the pharynx (Fig. 2) that is often considered homologous to the endostyle of *Amphioxus* but this homology is questionable. The subpharyngeal gland has no endocrine functions but gives rise to the adult thyroid gland which has an endocrine function.

Class Placodermi (Aphetohyoidea)

The Placodermi are a group of widely divergent archaic fishes appearing in the Silurian period (p. 34) and possibly as early as the Ordovician period. Although differing greatly in appearance they possess several common characters. The first gill cleft, which in the sharks forms a spiracle, bears a complete and functional gill. The hyoid or second gill arch is complete with gill rakers and takes no part in the suspension of the jaws. Jaw-like structures are present. Bone appears in the internal skeleton as well as in the heavy external

plates. Some also have bony scales of a ganoid type. Most of them show an operculum or flap covering the gills. Paired pectoral and pelvic fins of several types appear.

This class of fossil fishes includes the orders Acanthodii (Fig. 11), Arthrodira, Antiarchi, Petalichthyida, Rhenanida, and Palaeospondylia.

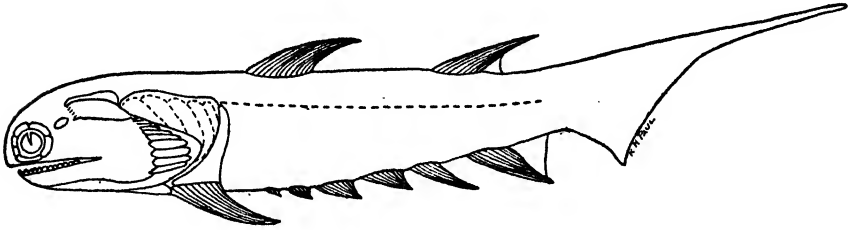


FIG. 11. An acanthodian shark, *Euthacanthus macnicoli*. After Watson.

dylia. They represent remarkable advances in several ways, marking the appearance of paired fins and of jaws, yet retaining the primitive character of a functional first gill cleft. They possess an operculum, a structure that is characteristic of the higher fishes. It is not clear that they were the ancestors of the higher bony fishes, and, although they may have been the ancestors of the sharks, they show many structures which are more advanced than those present in the sharks.



FIG. 12.

Class Chondrichthyes

The Chondrichthyes (Figs. 12, 13) are cartilaginous fishes with no bone in their skeletons. They appear late in the Devonian period and have persisted until present times, retaining many primitive structures. Their ancestors were probably some unknown placoderm group. They bear some resemblance to the Stegoselachians (armored sharks), a group of the placoderms of the lower Devonian, which looked some-

what like a skate or a ray but which had armored plates and scales and had the gills covered with an operculum—all of which did not appear in the sharks.

The jaws of the Chondrichthyes are formed from the first gill arch, which gives rise to the upper jaw (palatoquadrate) and to the lower

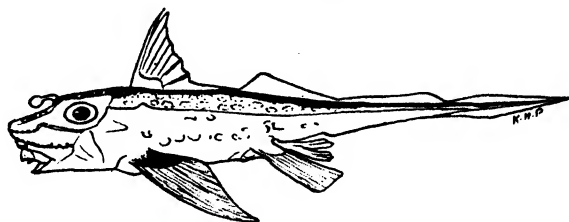


FIG. 13. *Chimaera*.

jaw (Meckel's cartilage). They have placoid scales mostly of dentine which became enlarged on the rim of the mouth, forming teeth. The intestine has formed a spiral valve arrangement which is apparently an early attempt to increase the absorptive area. No swim bladder is present. The paired pelvic and pectoral fins are well developed. The tail is typically heterocercal although some have modified this type.

The Chondrichthyes are divided into the subclass Elasmobranchii and the subclass Holocephali.

Classification of the Chondrichthyes

Subclass ELASMOBRANCHII. Gill clefts are uncovered; jaw suspension hyostylic; sharks, skates, and rays.

Order *Cladoselachii*. Very early and primitive fossil sharks. One of the most common is *Cladoselache* showing many primitive fish structures such as ventral ridges which seem to be horizontal "rudders" and which have been thought to give a clue to the origin of paired fins; has a terminal mouth, five gill clefts on each side, a heterocercal tail, typical shark teeth, and calcified vertebrae. Its well-defined fins seem to show how these structures were built up by the addition of skeletal elements, radials and basals, to the original base. The basal part, however, was still so broad and so closely attached to the body wall that it permitted little movement.

Order *Selachii*. Includes many fossil as well as living sharks. Gill clefts which range from five to six are not covered with an operculum. Many species of *Selachii* have been able to hold their

own in competition with the higher fishes. Modern sharks, representing end forms of an ancient stock, have lost many ancestral characters and some have become highly specialized. However, the general basic structures of a modern shark follow the basic primitive plan of a vertebrate, and for that reason the sharks are important in the study of vertebrate anatomy. Sharks have a world-wide distribution and are very numerous in bodies of salt water. A few species are able to live in fresh water.

Order *Batoidea*. Includes skates and rays, very much flattened fishes found in salt water. Although modified by their shape, their structure is fundamentally like that of the selachians.

Order *Pleurocanthodii*. Represented by only fossil species of which *Pleurocanthus* is best known. It was an early offshoot and was different from most sharks as it lived in fresh water. It was an elongated shark of the Carboniferous period, with a primitive terminal mouth, a diphyccercal tail, and primitive fins. It had teeth but seems to have been scaleless. The median fin extended from the anus around the tail and forward to the gill arches.

Subclass HOLOCEPHALI. Includes both fossil forms and the peculiar *Chimaeras* (Fig. 13) found at the present time in the sea. Gills covered with an operculum; a single narial opening; jaw suspension is autostylic. Their relationship to the sharks is questionable, and they may have evolved separately from some placoderm ancestor.

Class Osteichthyes

The Osteichthyes are fishes with skeletons partly or wholly of bone and are usually referred to as the bony fishes. They arose early in the Devonian period before the sharks; consequently they cannot be considered as descended from the Chondrichthyes as is often assumed. Their ancestry is doubtful; possibly they are from some placoderm group. The more primitive members of this class represent morphologically intermediate stages from cartilage to bone. The group became divided early into the subclass Actinopterygii or ray-finned fishes and the subclass Choanichthyes or nostril-breathing fishes.

Subclass ACTINOPTERYGII. The Actinopterygii include widely divergent fishes that extend from the Devonian period to the present. The vast number of present day bony fishes known as teleosts, are modern representatives of this group. The characteristic features of the group are paired fins without any basal lobed portion; one dorsal fin that may be divided; gill membranes usually supported by branchiostegal rays; and nasal sacs without internal openings. Bone, which was present in the

Placodermi or Aphetohyoidea, again appears. The lower mandible is formed by Meckel's cartilage covered by a sheath of dermal bones. Bony plates or a dermoecanium cover the chondrocranium. The pectoral or shoulder girdle contains some dermal bones and is often connected to the skull. A swim bladder is usually present.

The skeletons of the early actinopterygians were largely bone as is true of the highly specialized modern forms. The few primitive forms persisting today have retrogressed and have much of their skeletons unossified. The primitive ray-finned fishes are represented by the superorders Chondrostei, containing such forms as sturgeons, and the Holostei, containing the gars. A few species of these ancient groups still remain and, although highly specialized, show many body structures similar to the ancient Choanichthyes, a fact that indicates a close relationship in early times. The living representatives of these primitive superorders may be considered anatomically as intermediate forms between the modern teleosts and their questionable ancestors which were probably similar to ancient sharks but of a placoderm type. As these intermediate forms retain many primitive characters similar to those of the Choanichthyes which arose at a more or less contemporary period, they are of interest for the study of the origin of many tetrapod characters believed to be derived from the Choanichthyes.

These intermediate fishes were advanced over the sharks by the development of a number of structures that did not appear in the sharks. Many forms had great coats of bony armor and peculiar rhombic, ganoin-covered scales. Because of their hardness and their suitability for preservation, their fossils are the best preserved of all fishes. The swim bladder appeared and gave these fishes a great advantage, since it enabled them to use atmospheric oxygen in addition to that secured from the water by their gills. The few primitive descendants of these intermediate fishes show a cartilaginous skull (chondrocranium) surrounded by bony dermal plates. In *Amia* and in the gars various regions of the skull are partially ossified. The cartilaginous visceral bars used as jaws in the sharks are encrusted with bony dermal plates. The upper bar (palatoquadrate) no longer serves as an upper jaw but serves as part of the support for the bony dermal plates, the premaxilla and maxilla, which becomes the functional jaw of the actinopterygians. In the modern actinopterygians the bony plates on the head coalesce and become larger plates that sink under the skin and become incorporated with the chondrocranium which ossifies, thus forming the complete skull.

In the early forms the gular plates filled the space between the lower jaws, but these are now found only in a few representatives of the intermediate fishes, such as *Amia* and *Polypterus*, and in a few teleosts (*Albula*). The gills are covered by an operculum containing a series of four opercular bony plates. The intermediate fishes have a rather primitive vertebral column with a more or less complete notochord. In the higher actinopterygians the vertebrae have more complete centra and the notochord is constricted or pinched into remnants between the vertebrae.

Classification of the Actinopterygii

Superorder Chondrostei. This group extends back to the Devonian period (p. 34) and, although once extremely numerous, is now

represented by a few isolated remnants in different parts of the world.

Order *Palaeoniscoidea*. Fossil forms represented by *Cheirolepis* and *Catopterus*. This group shows the beginning of the evolution of modern fishes. They had a very efficient dental battery, large eyes, and were evidently carnivorous. Characterized by a single dorsal fin; a ganoid type of scale, rhomboid in shape with ganoin forming the outer layer; maxillary bone with a large expanded cheek plate; an opercular, preopercular, and subopercular; and numerous gulars. They were not large, but were usually from 1 to 3 feet in length.

Order *Acipenseroidi* (Fig. 14). Characterized by a well-ossified dermal skull; an unossified chondral skull; an endoskeleton

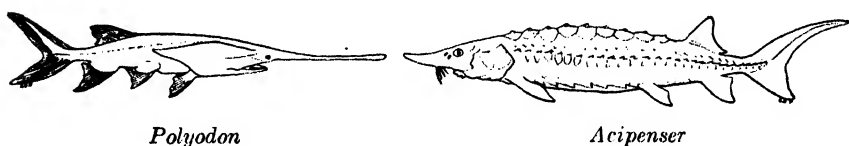


FIG. 14.

mostly of cartilage; if present, scales were either rhomboid or cycloid; tail, heterocercal; and dorsal swim bladder may be present. Notochord is but slightly constricted by the vertebrae. Spiral valve is present in the intestine. The order includes the sturgeons (*Acipenser*) and the paddlefish (*Polyodon*, Fig. 14, and *Psephurus*). The sturgeons, of which there are quite a few species, have the most extended range and live in a belt around the northern hemisphere. The paddlefish (*Polyodon spathula*) is found only in the Mississippi drainage, and the only other modern representative of the paddlefish (*Psephurus gladius*) is found in the Yangtze River in China.

Order *Polypterini*. Characterized by lobate pectoral fins with scaled bases; a well-ossified skeleton; rhomboid or cycloid scales; a constricted notochord; gular plates between the lower jaws; a spiracle; and the presence of both dorsal and ventral ribs. A spiral valve is present in the intestine. Swim bladder is alveolated and used as a lung. The only living representatives of this order are *Polypterus* and *Calamoichthys* (Fig. 15), both living in Africa. *Polypterus* is found in Lake Tanganyika, one of the oldest lakes in the world, and it is interesting because of the extruded

base of its lobed pectoral fins which once caused it to be considered a Crossopterygian.

Superorder *Holostei*. The holosteans, in point of time, follow the Chondrostei and precede the teleosts. Structurally this group continues the evolution of the fishes toward the teleost type and bridges



FIG. 15.

the gap between the Chondrostei and the Teleostei. The holosteans advanced in many respects above the condition of the Chondrostei. They developed much more bone in the skeletal system, especially in the skull, where the chondrocranium became strengthened by the development of bone centers; and the dermocranium and chondrocranium are partially joined to make a more compact structure. The holosteans lost the spiracle; retained a large swim bladder; and the tail, generally of the heterocercal type, is usually modified. Their scales were either rhomboid or cycloid.

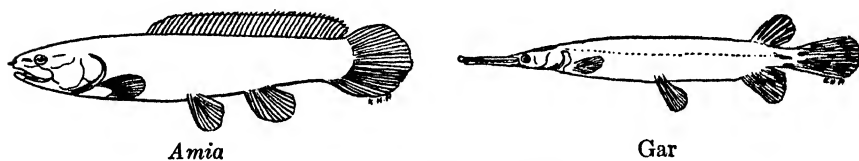


FIG. 16. Living Holostei.

The older forms are represented by *Semionotus*, *Dapedius*, and *Caturus*. Today the holosteans are represented by just two groups, the bowfin (*Amia calva*) and the family of the gars (*Lepisosteidae*) found only in America.

Amia calva is restricted to the eastern United States. The chondrocranium, although partly ossified, is not closely integrated with the bony plates of the dermal skull. This fish is covered with thin cycloid scales and has a modified heterocercal tail that superficially resembles the homocercal type. The large bilobed swim bladder with an alveolated lining serves as a very efficient organ of respiration (Fig. 16).

The gars or garpikes (*Lepisosteus*) are long-snouted fishes found in the eastern half of the United States and extending south into Mexico, Central America, and Cuba. One species, the alligator gar, reaches a length of fifteen to twenty feet in the southern states (Fig.

16). The dermal and chondral skulls are similar to those of *Amia*. Their long slender bodies are covered by a tight armor of rhomboid scales. Both *Amia* and *Lepisosteus* can live in water deficient in oxygen, as they can come to the surface and breathe freely with their swim bladders.

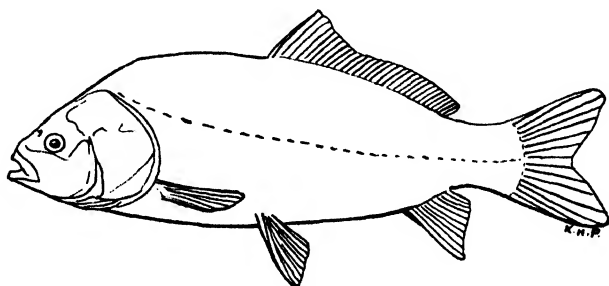


FIG. 17. Typical form of a teleost.

Superorder *Teleostei*. The teleosts (Figs. 17, 18, 19) are highly specialized and very successful fishes, able to live under practically every environmental condition to be found in water, and they have largely replaced the ancient strains in both fresh and salt water. They seem to have evolved at some time in the Triassic period (p. 34), probably from an old group, the Palaeoniscids; for their type was well established in the Jurassic period, and they became fairly abundant during this period. In the Cretaceous period they became very numerous, both in kinds and in individual numbers, and took the place which they have held ever since as the predominant type of fishes. They usually are covered with thin scales, either cycloid or ctenoid in shape, but a few scaleless forms are found. There is an extensive bone development, with good organization of the elements of the skull. The occipital region develops a supra-occipital bone, and there is a close union of the dermal and chondral elements. The notochord is reduced to a vestige, and the vertebrae are generally amphicoelous; that is, both ends of the body of the centrum are concave. A homocercal tail is formed by the addition of hypural bones (Fig. 167), and the fins lose some of their radials. A postclavicle series remains, by which the cleithrum and the pectoral girdle are attached to the skull. The gulars are lost, the vomer is single, and the bones of the lower jaw become simplified by a loss of a part of the plates or by the joining of some of the individual bones. They have a well-developed set of opercular bones. The swim bladder of the teleosts is mainly a hydrostatic organ, but in some (Physostomi) it is open to the esophagus and can be used

as an accessory organ of respiration. However, in many (Physoclisti) it is closed and serves mainly to regulate buoyancy. No spiral valve is present. The conus of the heart is reduced, and a muscular bulbus

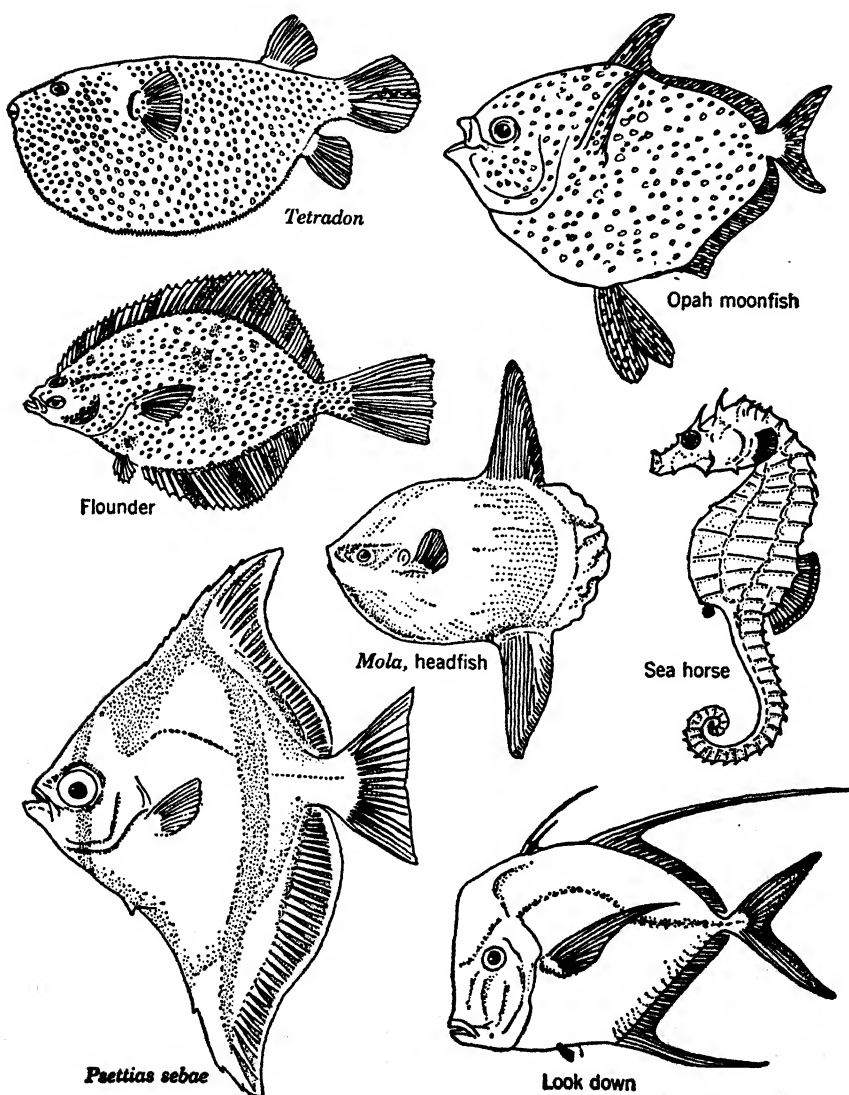


FIG. 18. Some of the body shapes in teleosts.

is developed at the base of the ventral aorta. The testes have developed special ducts separate from those of the kidney.

The number of existing species of teleosts is enormous. They have

developed into a wide variation of forms and to an extremely high degree of specialization. The teleosts are divided into two groups, the Isospondyli or soft-rayed and the Acanthopterygii or spiny-rayed fishes.

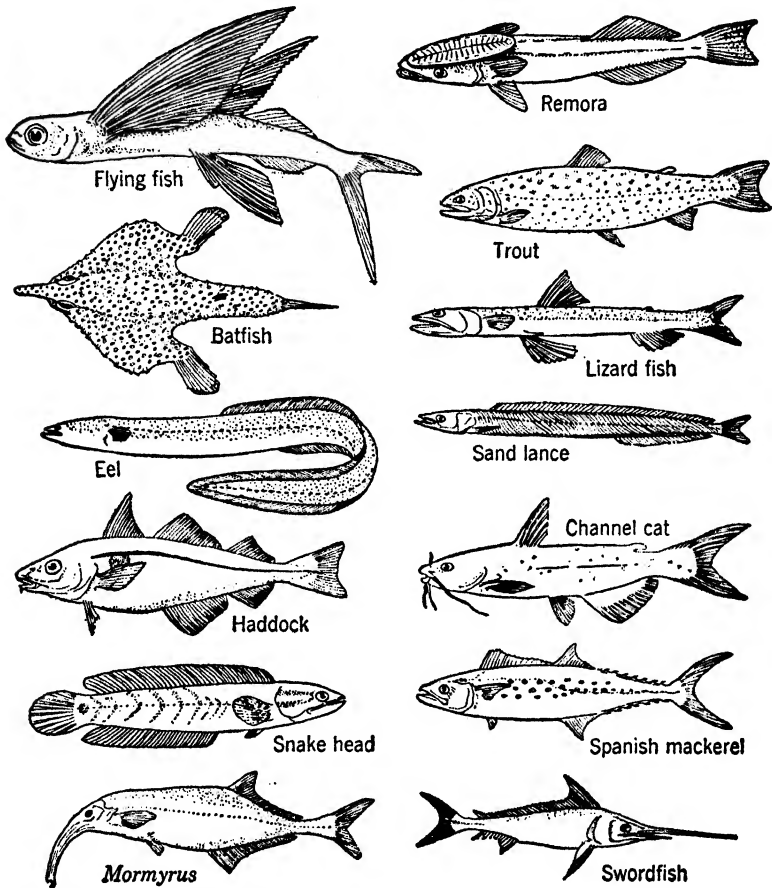


FIG. 19. Some of the body shapes in teleosts.

Subclass CHOANICHTHYES. The subclass Choanichthyes are fishes with nostrils opening through the roof of the mouth. The members of this group are important because they can breathe with their swim bladders as well as with their gills. This characteristic and the structure of their paired fins make them the probable fish ancestors of the land vertebrates. They possess paired fins which are either lobed or axial and differ radically from those of the Actinopterygii. They are a very ancient group and represent the earliest known fossil Osteichthyes. Only a very few members of this group exist today.

The Choanichthyes is divided into the superorders Crossopterygii and Dipnoi.

Superorder *Crossopterygii*. The Crossopterygii is perhaps the most important group of the Choanichthyes as they are the stem group from which the land vertebrates have evolved. The paired fins are lobed and bear some resemblance to a tetrapod limb. The jaw suspension is hyostylic. A spiracle is present. A number of fossil species are known. *Polypterus* and *Calamoichthys* from the Nile

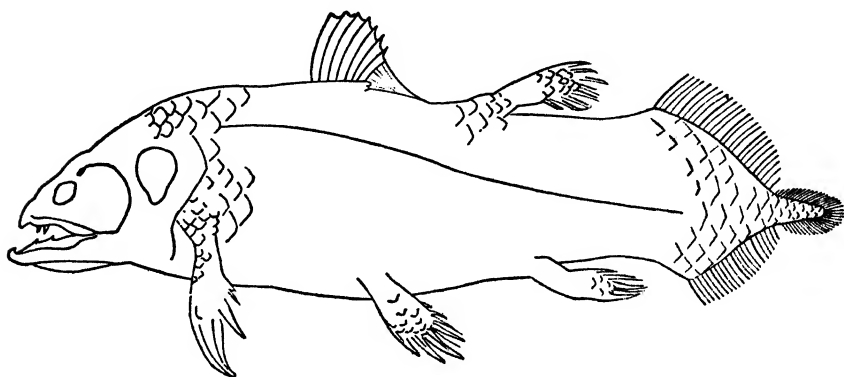


FIG. 20. *Latimeria chalumnae*, the living crossopterygian discovered in 1938.

were formerly included in this group but they were removed by Goodrich for anatomical reasons. *Osteolepis*, a well-known fossil species, has a superficial resemblance to *Palaeoniscus* (primitive Chondrostei) but has two dorsal fins, paired fins with fleshy lobes, and a tail fin with a small epichordal and a large hypochordal lobe. The skull bones have a different arrangement from those of *Palaeoniscus*. The crossopterygians, *Eusthenopteron* and *Sauripterus*, are of special interest to the comparative anatomist because their type of paired fins lend themselves to speculations on the origin of the tetrapod limb.

The order *Actinista* of the Crossopterygii has unusual interest because of the discovery in 1938 of a living Coelacanth, *Latimeria chalumnae* (Fig. 20), off the east African coast. This discovery proved the existence of a group of fishes that was thought to have become extinct in the Cretaceous period.

The fish was taken in a trawl Dec. 22, 1938, on the east coast of Africa, opposite New London. The trawl was dropped about 3 miles off shore in 37 fathoms of water. The coelacanth was at the bottom of a pile of about 4 tons of fish and remained alive for 3 hours after being taken on deck. The animal reached a taxidermist in about 24 hours and was prepared for "stuffing." No parts were saved, and material of inestimable value was thrown away or destroyed. Fishermen report that other specimens have been taken but that

they have been thrown back because of their strangeness and supposed uselessness. It is conjectured that this fish lived in deep water, but not the abyss, for it would have been dead when the trawl was taken up if it had been a real deep-water fish. It was a predaceous fish and a fairly active animal, probably crawling among the rocks with its peculiar fins. *Latimeria* made the front pages of almost every newspaper and magazine in the world and, for once, fish news became important. The specimen is now preserved in an African museum. It is about 60 inches long and bright blue in color. Unfortunately little more than the skin and bones were secured. The tail is distinctive since, besides the usual dorsal and ventral lobes, it has a third lobe between the other two. The swim bladder is calcified in the fossil forms. It is interesting to compare a restoration of *Undina*, a Jurassic form, with the recent specimen and to see how accurate are these interpretations of fossils.



FIG. 21. Living Dipnoi.

Superorder *Dipnoi*. The Dipnoi, or lungfishes (Fig. 21), were formerly regarded as ancestral to the amphibians but now are generally considered as being too specialized because of their peculiar dentition and other characters. They constitute an extremely old group distributed over the whole world in the early history of fishes, as shown by numerous fossils. Their skull is covered with bone, but the arrangement of the plates does not resemble closely that of the amphibians. Much of the chondrocranium remains cartilage, and the palatoquadrate has grown fast to the skull and no longer is in line with the upper jaw. No pineal foramen is present. Their jaw suspension is autostylic. They possess highly specialized dental plates instead of teeth. The paired fins are lobate with biserial rays on a long-scaled axis. The spiral valve of the intestines is retained, but the spiracle is lost. The most specialized organ is the swim bladder, which is highly vascular and is used as a lung when the water becomes low in oxygen content or dries up. There is a return of blood to the heart, the swim bladder being supplied by a branch of the sixth arterial arch, in contrast to other forms with swim bladders in which the supply of blood comes from the aorta (Fig. 256). A partial separation of the atrium has occurred as in the amphibians.

The modern representatives of the Dipnoi (Fig. 21) are found in three very widely separated regions of the world: *Neoceratodus* in a restricted part of Australia, *Protopterus* in the Nile drainage of Africa, and *Lepidosiren* in South America. This great separation of the living forms would supply a serious problem of distribution if

nothing were known of the geological history of the group and its former universal distribution. They are able to care for themselves under conditions in which other fishes would quickly perish. *Protopterus* and *Lepidosiren* bury themselves in the mud during drouths and breathe by means of their swim bladders, through openings connecting their burrows with the surface. *Neoceratodus* gulps air when the water conditions are not suited for branchial respiration.

Specialized Structures of Fishes

Fishes as a class make up a large part of the vertebrate fauna of the present day, although they are an ancient group that was present at a very early period of the world's history. Their persistence and their diversification prove that they are very well adapted to the environment in which they live. Their many new structures have better fitted them for a more active water life than was possible to their protochordate ancestors. One of their first needs was better locomotion. Developing from a median fold, the tail fin aided in locomotion after the posterior end of the body had been better supplied with skeletal and muscular parts that enabled it to become the main propelling structure. The covering of scales supplied the means of lessening the resistance of the water in their movements and also served for other purposes such as protection against injury.

The many varieties of body shape exhibited by fishes are closely correlated with the particular types of aquatic environment in which they live and with their activities. Sluggish forms that live on the bottom, such as rays, flounders, etc., are flattened or rounded; and their movements are necessarily slow and deliberate. Those that move about freely in the water, either searching for food or escaping from their enemies, have more of the fusiform shape with an approach to proper stream lines. Predaceous fishes of the highest type, such as mackerel, trout, salmon, pike, and other fast hunting forms, use every means to develop the highest speed, and these have trim, elongated bodies, well-developed tail fins, and high specializations of the posterior part of the skeleton and its musculature. See Figs. 18, 19.

An elementary survey of living fishes reveals a most bewildering array of specialized structures, many of which assist them in self-preservation or in food-getting. It is not surprising that these close adaptations should have developed, when one considers the great variety of environments available for fish life. These may be divided into two general classes, fresh water and salt water, each requiring a different physiological balance. In each we find a wide range of temperature and depth. Some are still waters, as in lakes, ponds, and

lagoons; others moving waters, with variable speeds, from sluggish streams to rushing torrents requiring a maximum of muscular development. Then there are many varieties of bottom, different kinds of aquatic vegetation, and other changeable conditions. The food of all young fishes and a few adults consists of plankton, the microscopic plants and animals to be strained out of the water by various devices; the adults of most species feed on vegetation, water-living invertebrates, and smaller fishes. The specialized structures of each species should be considered in relation to its particular habitat and its habits.

Ancient fishes gave rise to two main stocks. One stock developed the teleosts, which represent most of our present bony fishes and is an end product of evolution forming the highest and most specialized group of aquatic vertebrates. From the other stock arose the Choanichthyes from which the crossopterygians gave rise to the ancient amphibians from which the land vertebrates have evolved.

Review of Fishes

Fishes first appeared in the Silurian period and reached their maximum development in the Devonian and Mississippian periods. The ancestors of fishes were soft-bodied animals, somewhat resembling ammocoetes or *Amphioxus*. They had a sucking, jawless mouth, with cilia to aid in getting food to the digestive tract. The first sharks had a terminal mouth and lappet-like fins with broad bases, which permitted little movement. Armored fishes with bony plates on the body and head even preceded the sharks. Lungfishes developed a swim bladder as an aid in breathing. The highest fishes, the teleosts, appeared in the Jurassic period, rather late in geological history. Their skeleton typically is almost completely ossified, not cartilaginous. Fish scales are of four types: placoid, ganoid, cycloid, and ctenoid. The pectoral and pelvic fins are in pairs, and there is a variable number of azygous, or median, fins. All have the same structural pattern. The lobe fin of the type found in *Sauripterus* probably gave rise to the tetrapod limb. The chondrocranium is the protective skull built around the brain and sense organs. The visceral arches, migrating forward, formed the basis for the mandibular and hyoid arches. Dermal plates gave the skull its investing bones. The digestive system is short in carnivorous fishes and long and coiled in herbivorous fishes. A spiral valve, which increases the absorptive surface, is present in the lower fishes. The teeth are usually peg like and are ankylosed to the jaw. The tongue is not well developed. Respiration is carried on by gills, although swim bladders may assist, as in lungfishes. The swim bladder is present in all but a few bottom forms, and its function is chiefly hydrostatic. Those in which the duct connecting the swim bladder to the digestive tube is closed are termed Physoclisti; those in which the duct remains open are termed Physostomi. Weberian ossicles, a chain of small bones found in cypriniform fishes, connect the swim bladder with the nervous system. In the great majority of fishes the blood does not return to the heart after going through the gills, but in lungfishes there is a slight return of blood directly to the heart. The fish heart consists of two chambers, the atrium and the ventricle, with accessory chambers, the sinus venosus, and the conus.

Waste material is removed from the blood by the mesonephros, or kidney. The glomeruli of the Malpighian corpuscles are supplied with arterial blood, but a large amount of blood comes through the renal portal system and passes into the capillaries around the tubules of the mesonephros. In the lower fishes the spermatozoa generally escape from the body through the Wolffian duct, but in females the excretory and reproductive ducts are separate, the oviduct, or Müllerian duct, carrying the eggs to the outside. Teleosts develop other structures to carry the sperm and the eggs. Fishes are usually oviparous, laying eggs that are fertilized in the water, but some are viviparous, their eggs being fertilized internally. The brain of fishes is composed of five divisions and is very small in proportion to the size of the body. Those parts of the brain associated with the sense organs are comparatively large. The normal number of cranial nerves is ten. The sense organs, adapted for underwater use, normally operate only at close range, but many forms have a greatly extended use of these special structures. Lateral-line organs are usually prominent.

CHAPTER FOUR

Superclass Tetrapoda

The Tetrapoda includes all the four-footed land vertebrates. Definite fore and hind limbs have developed instead of paired fins. The feet or hands are typically constructed on a plan of five digits. The skull is greatly simplified by loss of the bones supporting the gills and by the fusion of others. The ear is improved by the modification of the spiracle to form the middle ear and by the inclusion of the hyomandibular to form the stapes. The pelvic and pectoral girdles assume form and structure capable of bearing weight on land. The lungs are highly developed, and all except a few land vertebrates depend on them for respiration. The body develops a neck in addition to the trunk and caudal regions already present. Originally the body was covered with scales and bony plates. These are retained in the lower forms, although some have lost them, but are mostly replaced by feathers and hair in higher forms.

The tetrapods arose from crossopterygians which developed into the early amphibians. From some of these early amphibians the modern amphibians evolved, and others gave rise to the ancient reptiles. The ancient reptiles developed into a great variety of forms which once dominated the earth. Many of them became extinct, but a few remnants remain today as the modern reptiles; others evolved into the birds and mammals.

Class Amphibia

The first land vertebrates were amphibians that made their appearance in the Devonian period when great changes were taking place on the surface of the earth. A single footprint about four inches long, of *Thinopus antiquus*, is the earliest known track of an amphibian. The Devonian oceans were subject to much shifting, as new land areas were pushed up, so that extensive bogs, swamps, and marshes were formed. This changing character of the environment presented difficult problems to the animals accustomed to living in water areas. Many of the marshes dried up by a slow process, and the swamps

became stagnant and were filled with dense masses of vegetation. The constant filling of the smaller areas of water and the exhaustion of their supply of oxygen made them less and less suitable for animals with gill respiration. Fishes such as the crossopterygians with open swim bladders could live where others were not able to endure the new conditions. While some fishes had become too highly specialized to survive, others were able to adjust themselves to these conditions, but a new system of respiration was necessary for the animals that were to survive on land.

Many of the lobe-finned crossopterygian fishes were not highly specialized and consequently had lost nothing that might be needed later. They already had characters that made them able to adjust themselves to new conditions. The swim bladder was connected with the gullet by a large tube and had an ample blood supply; its interior became alveolated and filled with small chambers supplied with capillaries, thus increasing the facility for the exchange of gases. The hard, scaly coat of these early forms, though making them rather unwieldy, prevented the rapid drying of the skin, and with a little adjustment it enabled them to make short excursions on land, from one water-hole to another. The skeleton, since it was already ossified, provided the necessary support on land. The fins, with their narrow, extruded bases, were of value in these first overland trips. The plan of the fin was such that, by slight modification, it could be made to bear some weight.

With the utilization of the swim bladder and the eventual obliteration of the gills, a reorganization occurred in the circulatory system. The single atrium divided into two chambers, and the ventricle developed separating flaps that helped in keeping the two bloods somewhat separate. The nervous system kept pace with the new developments, and changes occurred that enabled the amphibians to meet better the new conditions of land life. Changes occurred in all the sense organs, making them suitable for land life.

General Characteristics of the Amphibians

The structures of the amphibians were developed from those of the crossopterygian fishes that had already progressed a long way towards land life. The adjustments of the amphibians to the requirements of life on land is apparent in the division of the axial skeleton into regions, the strengthening of the connections between its parts, and the development of limbs, which replace the fins of fishes. The girdles of the limbs are organized to some extent to support the weight of the body. There is a striking reduction in the bones of the skull, particularly in those supporting and protecting the gills. The myotomic arrangement of the muscles is retained to a high degree, especially in the tailed forms. The early amphibians had bony dermal plates and scales, but modern

amphibia have smooth skins. The skin is thin, and there is a large cutaneous circulation. The digestive tract is rather simple. The tongue and oral glands are well developed in land forms. The lungs are thin walled and are not extensively divided by septa; being unable to carry on all the work of respiration, they are assisted by the cutaneous circulation. The heart is three chambered, as a septum divides the atrium into two chambers, one for venous blood and the other for blood from the lungs. The aortic arches are reduced in number; the sixth is used as the pulmonary artery, and the fourth is specialized to form the systemic artery. The venous system is changed by a postcava replacing the postcardinals and by the union of the lateral abdominals, which now return blood to the heart through the liver. The nervous system is somewhat changed from fish conditions by the slight invasion of the roof of the telencephalon by nerve cells. The autonomic system becomes prominent. The nose is connected to the mouth posteriorly, and the glottis is somewhat improved by the addition of strengthening cartilages. The eye has better means of focusing, although the lens is still round as in fishes. A middle ear is added, derived from the fish spiracle; a stapes is formed from the hyomandibular bone of the fish; an opening, the tuba auditiva, connects the middle ear with the pharynx; and a tympanic membrane may be present. The organs of excretion are of the mesonephric type. An adrenal gland becomes prominent at the anterior end of the mesonephros. In males the Wolffian, or mesonephric, duct carries both the spermatid fluid and the urine, but in females this duct carries only the urine, since the oviduct is a separate tube. Fertilization is usually external, although internal fertilization by means of spermatophores picked up by the females is common in tailed forms. A few amphibians are ovoviviparous. All undergo metamorphosis, although a few have pushed the tadpole stage back into the egg stage and, in this way, have freed themselves from water.

Metamorphosis

The Amphibia have never entirely lost their contact with water life, and in reproduction practically all, even those that live on land, go back to the water to lay their eggs. The few modern amphibians that have lost the habit of laying their eggs in water still develop the tadpole stage while in the egg. The eggs are laid in water in different ways; toads lay theirs in double strings; frogs lay theirs in masses; *Ambystoma* deposits them singly on bits of vegetation; and *Necturus* attaches them under bits of wood and under rocks. Most amphibian eggs are heavily pigmented but have a limited amount of food in the yolk. The young hatch in a few days and at first have little of the appearance of tetrapods, since most of the development comes later. The young live on the yolk for a time, finally getting a functional mouth and being able to take other food, usually vegetable matter. The growth continues, and the larvae now resemble a fish with three external gills, which serve in respiration. The organization of the muscles is fish-like, with evident myotomes and a tail used as a propeller. The fish-like circulation is retained in those that remain in water, but it becomes somewhat modified in those with lungs. The intestine, which is long and well coiled in the young stages, is much shorter in relation to the body length of the adult. Forms leaving the water approach land conditions gradually, with developing limbs and changes in the circulation that throw more and more responsibility on the lungs, until finally the gills are absorbed, the clefts are closed, and the adult stage is reached.

Classification of the Amphibia

The most recent classification (Romer, 1945) divides the amphibians into two subclasses, the Apsidospondyli and the Lepospondyli. These include both fossil and living species. Formerly the term *Stegocephalia* was used to include most of the fossil forms. It included a heterogeneous group of forms which were but distantly related and hence is not a satisfactory taxonomic term.

Subclass APSIDOSPONDYLI. Characterized by the vertebrae in which the centra seem to be formed from blocks or arches of cartilage.

Superorder *Labyrinthodonta*. Contains a number of very primitive orders of extinct amphibians; probably contains the first tetrapods. Characterized by an armor of scales.

Order *Ichthyostegalia*. Oldest and most primitive tetrapods. Described from the Devonian deposits of Greenland. Although only the skull is known, this group has retained several structures and conditions which connect it closely with the fishes. Arrangement of the bones of the skull roof and palate resembles that of the Choanichthyes. External nares are on ventral side of skull; there is a persistent preopercular bone; the lateral-line canals are covered with bone. This is an important group in the phylogeny of the amphibians.



FIG. 22.

Order *Rhachitomi*. Common Permian amphibians containing the well-known *Eryops* and *Cacops* (Fig. 22). Some had a dermal armor.

Order *Stereospondyli*. Degenerate forms from the Upper Permian and the Triassic periods; possessed a centrum formed entirely by the hypocentrum.

Order *Embolomeri*. Primitive forms showing some structures suggesting relationship to the early reptiles; limbs were poorly developed; became extinct at the beginning of the Permian period.

Order *Seymouriamorpha*. Lower Permian period. Well-known *Seymouria*, often considered a primitive reptile, has now been

placed here (Romer, 1945). Possessed a combination of reptilian and amphibian characters; well-developed girdles and limbs. Centra formed by large pleurocentra and wedge-shaped hypocentra.

Superorder *Salentia*. Highly developed fossil amphibians.

Order *Proanura*.



FIG. 23. *Rana*.

Order *Eoanura*.

Order *Anura*. Highly specialized modern amphibians without tails except in larval stages; sternum and girdles highly specialized; visceral skeleton reduced; skin somewhat hardened in toads, but alive and glandular in frogs; specialization of the vertebrae, pelvic girdle, and limbs for locomotion. *Bufo* (toads), *Rana*, Fig. 23 (frogs).

Subclass LEPOSPONDYLI. The subclass Lepospondyli is characterized by having the centra formed as bony cylinders arising around the notochord. This group includes three extinct fossil orders and two living orders.

Order *Aristopoda*. A group of extinct limbless forms.

Order *Nectridia*. Fossil forms which have very small limbs or are without limbs.

Order *Microsauria*. Very small fossil forms which are probably related to the modern Urodeles and Apodes.

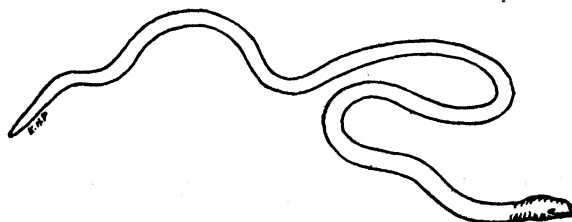


FIG. 24. *Caecilia*.

Order *Apoda* or *Gymnophiona* (Fig. 24). A group of legless snake-like forms found in the tropics. Their eyes are reduced or lost. Only modern amphibians possessing scales which are minute and buried in skin. Represented by such forms as *Caecilia* (Fig. 24), *Ichthyophis*, *Herpeles*, and *Siphonops*.

Order *Urodela*. A large group of modern amphibians with four legs and tails, includes salamanders and newts (Fig. 25). In some respects the urodeles have not advanced far beyond the conditions of a primitive amphibian, and their ancestry probably leads back to some of the early lepospondyls. *Hylaeobatrachus* of the Wealdon of Belgium from the Lower Cretaceous period is one of the earliest urodeles. All the modern groups of the urodeles have been differ-

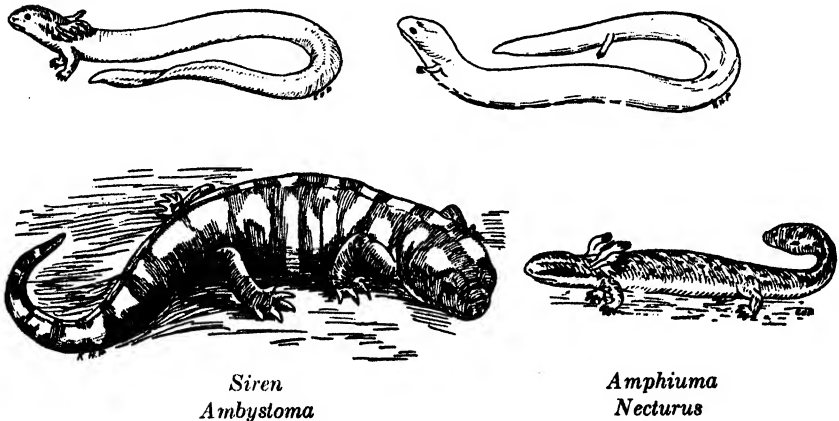


FIG. 25.

entiated since Cretaceous times. They are widely scattered geographically, being found on all the large land masses and on many islands. The general body form of the urodeles is primitive. Their skeleton contains much cartilage and probably represents considerable retrogression rather than a primitive condition. Their branchial structures are well developed in the larval stage and in some, such as *Necturus*, are retained for life. The circulatory system of the gill-breathing forms retains many primitive characters and serves to represent an intermediate stage between fishes and land vertebrates.

Class Reptilia

The reptiles are an important group because of their own wonderful variability and because of the fact that they supply the intermediate link between the birds on one hand and the mammals on the other. The first known reptiles appeared in the upper Carboniferous, or Pennsylvanian period, but it is probable that their actual separation from the amphibians came in the Devonian period. The earliest reptiles were much like the early labyrinthodonts, and from anatomical evidence it appears that they were closely related. *Seymouria*, one of

the labyrinthodonts, resembled closely the earliest cotylosaurs, a stem group of the primitive reptiles. The skull of *Scymouria* was of the solid type with no openings, or arcades, except those for the nose, eyes, and parietal eye, and the notches for the ears.

General Characteristics of the Reptiles

The reptiles arose early from the amphibians and became true land animals, a condition never quite reached by the amphibians. The amphibians already had developed some structures necessary to fit them for land life, but many further modifications were made by the reptiles. The skin of the amphibians was moist, as in the fishes, but the skin of the reptiles became dry because of the development of an outer layer of dead epidermis that was thickened and horny and had lost its mucous glands. In other words, the body was separated from the air by a layer of cornified epithelium that prevented evaporation. Generally the covering was made up of scales or plates of bone, although a few reptiles on reverting to the water lost this covering and became smooth skinned again, particularly the ichthyosaurs and the soft-shelled turtles.

The skeletal changes came slowly, since the earliest reptiles were not much better in this respect than the labyrinthodonts. The cotylosaurs and other early forms had many points in common with the early amphibians, especially in the skeleton. Before the highest reptile stage was reached, the skull lost some of its elements and many changes were made in the parts concerned with locomotion. The vertebral column was further differentiated in all its parts. The ribs of some were reduced in the cervical and lumbar regions. The cervical region became more pliable by a refinement of its joints, and its first two vertebrae, the atlas and axis, became highly specialized to supply a more flexible joint with the skull. A well-developed sternum attached to the ribs appeared and gave some assistance in forming a brace for the anterior girdle. The posterior girdle was also strengthened and its individual elements improved, so that they were better able to support the body. The limbs acquired better joints where movement was required, and the increasing specialization of muscles and nerves gave them better coordination. The toes were tipped with claws that were very useful in land life, especially for such purposes as climbing and digging, and served as a protection to the ends of the toes in walking. The visceral arches were reduced to a hyoid series representing from two to four arches.

As the reptile scale is ascended there is a progressive loss of the bones of the skull, either by elimination or by joining with other elements. The parasphenoid, striking as a landmark of the fishes and amphibians, becomes reduced or absent. There is a tendency toward the opening of the skull roof by the formation of arcades, so well shown in *Sphenodon* (Fig. 27). Instead of two occipital condyles, as in living amphibians, the modern reptiles have only one. Well-developed sclerotic bones appear in the eyeball of many reptiles. Some have a parietal foramen in the skull.

The reptiles have a more advanced central nervous system than the amphibians. Parts of the brain are somewhat enlarged and the fiber connections are multiplied, thus making a better synchronized and coordinated brain. The lateral-line system is entirely lost but the eye, nose, and ear become better developed. Better musculature is developed in the reptiles. Instead of mass

action of parts, there is a finer division of function and a more individual use of the different muscles, as in the toes and fingers. The earlier reptiles acquired extra nerve material to supply the huge development of the shoulder and hip regions by enlarged spinal cords. The brain eventually became enlarged in its relation to the body weight of later reptiles, with a decided increase in the size of the forebrain and a corresponding increase in the connections with the posterior part of the brain and the spinal cord.

The pallium, which was invaded by a small number of nerve cells in the amphibians, now has a large number of neurons. The cerebrum is large and swollen in comparison to that of the amphibians and has many more tracts between it and the rest of the brain. The corpus striatum is enlarged in size and in importance. The diencephalon becomes covered by the growth of the cerebrum and by the optic lobes, so that it does not show from the dorsal side of the brain at all. The cerebellum is variable, not strikingly large, and with flocculi in the higher forms. Two more cranial nerves, the eleventh and twelfth, are taken into the skull cavity and added to those already there. (Snakes still have but ten.)

The digestive system in reptiles is rather simple and not much advanced over conditions found in the amphibians. The stomach is long and spindle shaped in the Lacertilia, as in *Ambystoma*; the duodenum is short, with the entering ducts of the liver and pancreas marking its distal limit. The pancreas is wedged between the duodenum and the stomach. The intestine is not very long, and it ends abruptly in a large rectum, which in turn enters the cloaca. As in *Ambystoma*, there is a great difference in the diameter of the lower end of the intestine and the rectum. The stomach becomes more complicated in the higher reptiles, and some ancient reptiles developed a gizzard or grinding mill, a device retained by some birds. Little piles of highly polished pebbles, often associated with the stomach region of fossil dinosaurs, are now known as gizzard stones or gastroliths.

The lungs increase in size and diameter, and their internal structure is much modified by the building of a series of partitions extending the length of the lung, which greatly increase its capacity. The glottis is made more efficient by the addition of parts to improve its action. With further development of the larynx, the trachea becomes ringed with semicircular cartilages to prevent its collapse in breathing. The intake of the air is through the nostrils, or external nares, then into the pharynx through the internal nares. Instead of depending on the mouth and throat for forcing the air into the lungs, assistance is now given by the ribs and intercostal muscles.

With the loss of the branchial circulation, the fifth aortic arch drops out entirely, the third functions as a part of the carotid, the fourth as the systemic, and the sixth as the pulmonary. The heart improves, and there is a partial division of its ventricle (complete in the Crocodilia and probably complete in the Pterodactyla). The arterial system remains much the same, but the venous system makes a number of changes, bringing it more to the right side of the body and removing it from the symmetrical plan of the sharks. New vessels appear and old ones are enlarged. The postcava, which was a new vessel in the amphibians, becomes the main passageway for the blood that formerly went through the postcardinals. The renal portal system is being reduced and of much less importance than in the amphibians.

The kidneys: the Rhyer of the metanephric type found in birds and mammals, and; the Crocodilia, have been lost, and there is no opening into the

coelom. The ureter, a new vessel, conducts the urine from the kidneys; and the old mesonephric, or Wolffian duct, is now used in the males for the transmission of spermatozoa and is vestigial in the females.

Numerous changes occurred in details of the reproductive system, all associated with land life. Real independence came to the vertebrates with the development of the reptilian egg, which no longer necessitated a return to water for reproduction. With land life, fertilization became necessarily internal and some sort of intromittent organ, such as the penis, is developed for the introduction of the spermatozoa into the cloaca of the female. The egg is much larger than in amphibians, with more food supplied for growth and development of the embryo. In the oviparous forms there is either a leathery or chalky shell to protect the egg from drying and injury. All the rattlesnakes and gartersnakes, most of the horned toads, a number of lacertilians, and the extinct ichthyosaurs are known to bear living young (ovoviviparous).

Two embryonic membranes, the amnion and the allantois, appear for the first time in the reptiles. Since they are also found in birds and mammals as well as reptiles, the name *Amniota* is sometimes applied to these three classes. The first membrane, or amnion, is a protective structure that surrounds the embryo, enclosing it in a fluid. The amnion is formed by the embryo from the material of its own body. The allantois, the second membrane, is also developed by the embryo and is used for respiration. In the placental mammals it becomes a very highly specialized structure for the transfer of food from the mother to the young and for the removal of waste. With these improved means of reproduction the reptiles have advanced far ahead of the amphibians.

Extinct Reptiles

In the Mesozoic era the reptiles evolved into a bewildering assemblage of powerful creatures that dominated the world. They became highly specialized and able to live in many different habitats, including water and air. The return to the sea was made by the mesosaurs, plesiosaurs, crocodiles, snakes, turtles, and other forms, the most perfect water reptiles being the ichthyosaurs. Large groups inhabited the fresh water of rivers, swamps, and lakes but did not become so specialized as those that went to sea. Those that remained on land varied greatly in size and agility, some being only a few inches long and others more than a hundred feet. One of the best-known divisions is the dinosaur group, composed of carnivorous and herbivorous forms of many species and genera, which spread all over the world. *Brontosaurus*, *Diplodocus*, *Trachodon*, and *Triceratops* (Fig. 31) attained great weight and bulk. They lived at a time when food was abundant and easily obtained, and in a climate that was perfect for their best development. By the end of the Cretaceous period most of the reptile orders had died out, owing in part perhaps to changing climatic conditions and to changes in food conditions. Carnivorous dinosaurs, magnificent in every respect, were replaced by the more defenseless herbivorous reptiles. Instead of bipedal,

walking and jumping much as the kangaroo of today, and had small front limbs suited for handling food. *Tyrannosaurus* and *Allosaurus* (Fig. 31) were among the largest of the carnivorous forms.

Although possessing wonderful bodies, even the largest of the ancient reptiles had a comparatively small brain—thirty tons of muscle and bone controlled by a few pounds of nervous tissue. Some of the herbivorous forms, such as *Diplodocus* and *Stegosaurus*, developed a hip brain that was several times the weight of the head brain. Footprints of dinosaurs are very common in many parts of the world. The Connecticut River valley has large areas covered with hundreds of tracks. The finding of dinosaur eggs in the Gobi desert by Andrews was one of the most interesting discoveries of many years, for they were well preserved and gave some information of the home habits of the group.

The flying reptiles (Fig. 30), the pterosaurs or pterodactyls, were real fliers with bird-like air adaptations in their skeletal parts. The sternum and pectoral regions were adapted for the insertion of large flight muscles. The hand was modified for flying by the enormous elongation of the fifth digit, which supported the wing membrane. Light bones, thin and hollow-walled, completed their flying equipment. Again it seems probable that, with their activity, a four-chambered heart was present. They were very numerous and varied in size from a sparrow to those with a wingspread of thirty feet. Specimens have been found in Germany with the web of the wing intact, so that its texture is known. Evidently they were smooth skinned and without scales or plates.

The ancestral stocks of both the birds and the mammals lie somewhere in these extinct reptiles. The exact line of bird ancestry is not known, but it appears to come through the Pseudosuchia, a reptile group related to the pterosaurs, crocodiles, and dinosaurs. The mammalian stem seems more certain, the Therapsida of Africa and other continents offering an ancestral type that is very satisfactory. The cynodonts of Africa, the best known, have a jaw with an enlarged dentary and a reduced articular region. The reduction of the quadrate seems to indicate the possibility of a new jaw articulation in which the squamosal would form the articulating element. The discoveries of Richard Broom seem to make this derivation of the mammals positive.

Modern Reptiles

The reptiles of today comprise about 3500 species and are divided into five groups: the Rhynchocephalia, represented by *Sphenodon* of New Zealand; the Crocodilia, including the crocodiles and alligators;

the Chelonia, or turtles; the Lacertilia, or lizards; and the Ophidia, or snakes.

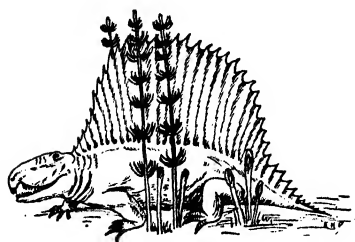
Sphenodon (Fig. 27) is a small reptile, living in a very restricted area of the world. It is a left-over from a former group that was once more numerous. The Crocodilia are the largest reptiles living today, since some of the sea forms attain a length of forty feet. The land tortoises and sea turtles also attain weights of a thousand pounds, but generally the Chelonia are not very large. The lizards and the snakes are numerous everywhere and are the predominant types of living reptiles. The Lacertilia, though generally small, include a few large forms, such as the Komodo lizard, of New Guinea, that reaches a length of thirteen feet. The monitors are about six feet in length. The Ophidia, or snakes, are very numerous, and some of the boas and pythons grow to a length of from twenty to thirty feet but such extremes are rare, and the largest are usually not much over twenty feet. Poisonous forms of the reptiles are confined to the snakes, with the exception of the Gila monster (*Heloderma suspectum*), which is the only known poisonous lizard. This lizard has a poison as dangerous as that of the rattlesnakes, but fortunately for man, its means of injecting the poison is poor, through grooved teeth in the lower jaw. This transmission of the poison is not satisfactory but is very effective on small animals which the lizard is able to twist around and chew.

There are two groups of poisonous snakes in the United States, the Crotalidae and the Elapidae. The Crotalidae include the well-known rattlesnakes, water moccasin, and copperhead, known as the pit vipers. They are provided with hollow fangs and are able to inject their poison into the tissues. The poison is not protective but is used to deaden their animal food and is very effective since a rat will become quiet in a few minutes if the poison is well injected so that it reaches the blood system. The paralyzed prey can then be swallowed with no danger to the snake. The crotaline venom attacks the blood system. The Elapidae have a single representative genus, the coral snakes of two species, found along the gulf coast and seldom more than four hundred miles from the coast. They are beautifully colored with cream, black, and scarlet and, although small and harmless in appearance, are very deadly. Their short, permanently erect fangs are capable of terrible execution if the opportunity offers. They are related to the cobra of India.

Classification of the Reptiles

Subclass ANAPSIDA. Primitive extinct reptiles (Permian to Triassic) in which the skull is completely roofed over.

Order *Cotylosauria*. Primitive extinct reptiles (Lower Pennsylvanian and Triassic) closely resembling the *Seymouriamorpha* of the primitive amphibians. They retained the cleithrum. This is the stem group of the reptiles. *Diadectes* (Fig. 26) belongs to this group.



Dimetrodon



Diadectes

FIG. 26.

Order *Chelonia*. Reptiles with a highly specialized skeleton, forming a carapace and plastron; usually covered with epidermal plates; vertebrae very variable; habitat on land, in fresh water, and salt water; skull resembles secondarily those of the lowest reptiles; jaws encased in horny shields, without teeth. Snapping turtles, soft-shelled turtles, box turtles, sea-turtles, etc.

Subclass *ICHTHYOPTERYGIA*. Extinct aquatic reptiles with fish-like bodies, caudal and dorsal fins. Limbs developed into paired fin-like structures.

Order *Ichthyosauria*. Extinct ichthyosaurs some of which reached a great size.

Subclass *SYNAPTOSAURIA*. A highly diversified extinct group; mostly aquatic or amphibious reptiles with a single pair of temporal openings in roof of skull.

Order *Protorosauria*. Extinct reptiles which were relatively small and agile.

Order *Sauropterygia*. Extinct reptiles with paddle-like limbs; some, such as plesiosaurs, were very large.

Subclass *LEPIDOSAURIA*. Reptiles with a diapsid type of skull, double pair of openings on roof and sides of skull separated by postorbito-squamosal arch, or modifications of this plan.

Order *Eosuchia*. Extinct small primitive reptiles; some were aquatic.

Order *Rhynchocephalia*. Reptiles with two arches in the skull, well-developed pineal eye, acrodont dentition; abdominal ribs present; reptiles represented by a number of extinct species but by only one modern form, living in New Zealand (Fig. 27); *Sphenodon punctatum* (common name Sphenodon or tuatara).



FIG. 27. *Sphenodon*.

Order *Squamata*. Body covered with scales or plates; ribs with single heads; no abdominal ribs; with movable quadrate; skull with a single temporal opening, apparently a modification of the diapsid type; many diverse types, both extinct and modern. The modern forms may be



FIG. 28. Ring-necked lizard.

divided into two suborders: the Lacertilia or lizards and the Ophidia or snakes.

Subclass ARCHOSAURIA. Rather advanced types with diapsid skull. Includes the great reptiles such as the huge extinct dinosaurs, the pterodactyls, and the crocodiles. Some developed a bipedal gait.

Order *Thecodontia*, primitive extinct archosaurs with teeth in sockets.

Order *Crocodylia*. Reptiles with a four-chambered heart; abdominal ribs; life in the water; thecodont teeth; secondary palate driving the posterior nares to the pharynx; no pineal opening. Living forms are alligator, crocodiles, gavials, caiman, etc. (Fig. 29).

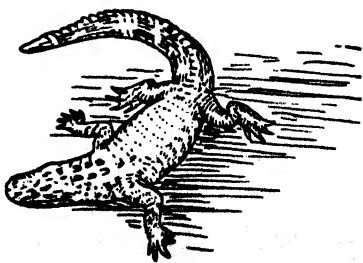


FIG. 29. Alligator.

Order *Pterosauria* (*Pterodactyla*). Flying reptiles of the Cretaceous period; hand modified for flying by elongation of the fifth digit; bones pneumatic. (Fig. 30) *Pteranodon*.

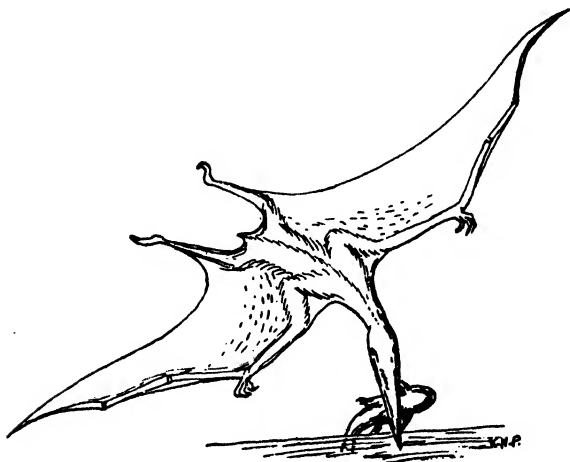


FIG. 30. Pterodactyl.

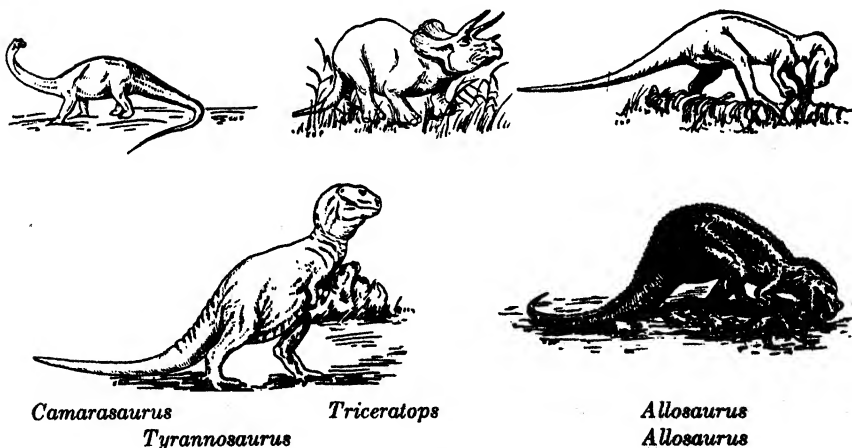


FIG. 31.

Order *Saurischia*.

Order *Ornithischia*. These last two orders are the extinct dinosaurs (Triassic to Upper Cretaceous periods); the largest, most grotesque, and most variable of all the reptiles.

Subclass SYNAPSIDA. Extinct mammal-like reptiles of the Permian and Triassic periods, with a single pair of lateral, temporal openings

in the skull, primarily ventral to the postorbito-squamosal arch. It is the group from which the mammals have been derived.

Order *Pelycosauria* (*Theromorpha*). Extinct reptiles representing the primitive synapsids. (Fig. 26) *Dimetrodon*.

Order *Therapsida*. Extinct reptiles in which the posterior bones of the mandible and the quadrate are greatly reduced; teeth may be divided into incisors, canines, premolars, and molars. Epipterygoid becomes part of braincase; stapes extends to quadrate. (Fig. 32) *Cynognathus*.

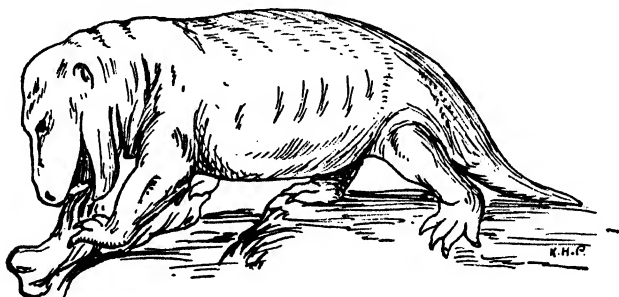


FIG. 32. *Cynognathus*.

Order *Ictiosauria*. Extinct reptiles which seem to be transitional types, sometimes referred to as primitive mammals. Dentaries are only conspicuous bones in jaw; other jaw bones are greatly reduced.

Class Aves (Birds)

The ancestry of birds leads back to the reptiles of the Mesozoic period, when a light-boned, large-brained, active group of the Pseudosuchia, related to the dinosaurs, pterodactyls, and crocodiles, developed a flying wing of the avian type. There are varying opinions as to whether the actual bird stem came up through an arboreal or a cursorial pre-bird ancestry, with the greatest weight of the argument for the arboreal, since it seems probable that an animal could get into the air by means of tree life more easily than by volplaning from the ground. In arboreal life, the fore limbs would be used at first for grasping, but by becoming webbed would give enough support for short sails through the air, and eventually lead to flight. By the development of feathers these intermediate forms were enabled to maintain a more stable temperature and to be more active. Early, there was a splitting into two branches, the running and the flying. Some writers have insisted that these two groups came from two origins instead of one, but this assump-

tion seems rather unnecessary, and there is little evidence to support it. From what is known of the earliest birds, the Saururæ, it is possible to have a wing serviceable for flight, and at the same time equally good for grasping limbs.

The first known birds appeared in the Jurassic period, and their remains have been found at Solenhofen, Germany. Two fairly complete specimens are known, *Archaeopteryx* (Fig. 33) at London and *Archaeornis* at Berlin. Some other fragments have been found, but these represent the only complete specimens. They were small, about the size of a crow, and covered with feathers in true bird fashion, but their anatomical features are about as close to the reptiles as to the modern birds. Naturally, they inherited a number of reptilian traits. Without the imprints of the feathers, these fossils would probably be placed in the doubtful class today.

The Archaeornithes, to which these two belong, differed from modern birds by having conical teeth, free fingers on the wing, no uncinatæ processes, neck ribs long and free, fingers with claws, tail long and composed of many vertebrae, each vertebra with a pair of feathers, sternum small, ribs needle-like and weak. The brain was small and reptile-like. Anatomically the skull is easily differentiated from modern birds but not so easily from the reptiles. The vertebrae were amphicoelous as in some of the later birds.

The next group of birds, the Odontognathæ, is represented by quite a number of specimens found in the Cretaceous period of Kansas. One of these, a diver, *Hesperornis regalis* (Fig. 34), was about four feet long with vestigial wings, a fine set of needle-like teeth, and amphicoelous vertebrae. A second water-bird, *Ichthyornis impar*, found a little later geologically, was also toothed, gull-like in appearance, and of medium size. It is highly probable that at this time birds were widely differentiated and generally distributed, but little is known of them since bird remains are so likely to be destroyed.

The birds of the Tertiary period were much like the birds of today, with about as many orders. From discoveries made in the asphaltum pits at Rancho de la Brea and in other places, the birds of this period are better known. The carinates and ratites existed in the Eocene period. *Diatryma*, a typical ratite form, was found in the United States, and in South America and in other parts of the world these walking birds must have been rather common. *Phororhacos*, frequently shown in books of bird history, was a hawk-like form with a head as large as that of a horse. It must have been a wrecker of the small mammalian fauna of the locality. *Aepyornis*, a wingless moa from Madagascar, was seventeen feet in height and laid an egg thirteen inches long and nine inches in diameter. The moa population of New Zealand was

very extensive, consisting of both large and small forms. The largest, *Dinornis maximus*, was about ten feet in height. The kiwi (Fig. 35), a modern representative, is about the size of a chicken. Today the walking birds are very limited in their distribution, being found in South American (rhea), Africa (ostrich), South Western Asia (ostrich), and Australia and New Zealand (emu, cassowary, kiwi). These are the last representatives, and they seem doomed to extinction with the gradual encroachments of civilization.

The carinates are very numerous, both in species and in individuals, and seem able to hold their own against most of the handicaps that man has placed upon them. They are very highly specialized and are able to live under most conditions, from the ice regions of the poles to the tropics. Some flightless forms have appeared, such as the penguin and the great auk.

General Characteristics of Birds

Birds have developed some stable characters found in no other group. For example, no other class has a covering that resembles feathers. These develop much as do the scales, but the final product is entirely different and perfectly distinctive. Scales are retained on the feet and legs of most birds. No member of the class has lost this coating, although parts of the feather may be lost, resulting in the hair-like covering of some of the flightless birds. The penguins, reverting to a water life, have scale-like feathers covering the wings. The single condyle of the skull is shared with the reptiles. The brain is much larger than that of any reptile. The body temperature regulation is good, but the temperature is not absolutely stable. A bird with a temperature of 112 degrees may live comfortably in a temperature of -30 degrees, because of the fine insulation, physiological activity, and the efficiency of the heat-regulating devices. Birds are entirely bipedal with the anterior limbs modified for flight, a character shared with some of the reptiles and mammals. Although teeth were present in ancient forms they are entirely lacking in modern birds. The mandible and maxillae are sheathed in a horny covering, forming the bill. The bones of the flying forms are light, pneumatic, and often connected with the lungs by ducts from the airsacs. The right ovary and its duct atrophies, leaving only a vestige. The heart has four chambers as in the mammals.

One anatomical peculiarity, the retention of the right aortic arch, differentiates birds from all other classes. The wings have retained but three digits in modern forms, and the feet have but four toes. There is a general similarity between the reptiles and birds, which extends to every part of their anatomy.

Every part of the bird skeleton is specialized for flight, with much fusion of bone to secure rigidity, strength, and stability.

The skull is fused into one piece in the adult. The only movable parts are the quadrate and mandible, except in parrots and a few others in which the maxilla is movable. The skull is very light, even in large-headed birds such as the toucans and pelicans. The long slender jugal and quadrate-jugal, and the large brain case, serve to separate birds from reptiles. The brain is covered anteriorly by the ossification of the lateral sphenoids. The elongated anterior part of the skull is formed by the prolongation of the facial elements,

thus forming the beak. The pineal foramen has disappeared, the eye sockets are large, and the palate is open in contrast to the solid structure of most reptiles.

The vertebral column is specialized for flight, with the elements fixed in a rigid manner, so that the mechanics of flying are not interfered with by loose parts. The neck vertebrae are numerous and quite pliable, with small ribs joined to the vertebrae. All modern birds have vertebrae with saddle-shaped ends of the centra. The vertebrae in the thoracic region are joined together by ossified tendons. The lumbar, sacral, and a part of the caudals are ankylosed together to form a synsacrum, which is covered by the greatly enlarged ilium. The type of the pelvis is the same as that found in bipedal reptiles. The ribs are rather stocky and fastened together by uncinate processes. A well-developed series of sternal ribs attach the ribs to the sternum, forming a solid basis for the insertion of flight muscles. The shoulder girdle forms a triangle, with the humerus articulating at the apex. The coracoids act as a brace for the sternum. The carinate sternum is made distinctive by a large keel to which the pectoral muscles are attached. The vertebrae and the ribs, thus connected with the sternum, form a complete bony ring that is comparatively rigid. The anterior limbs are modified for flight by consolidation and reduction of parts in the carpus and manus.

The posterior limbs have a number of characters in common with the bipedal dinosaurs. The tibia is large, and the fibula reduced to a splint. The tarsal bones fuse with the tibia and metatarsals to form an intertarsal joint. The tibia, fused with the proximal series of tarsal bones, forms the tibiotarsus.

Classification of Birds

Subclass ARCHAEOORNITHES. The most primitive known birds, in the Jurassic period; skeleton reptile-like; vertebrae amphicoelous; tail long, with a pair of feathers on each of its vertebra; sternum small or rudimentary; ribs needle-like, with no uncinate processes; fore limbs modified as wings, but with three clawed digits free; neck ribs present and free. (Fig. 33) *Archaeopteryx* and *Archaeornis*.

Subclass NEORNITHES. Tail vertebrae reduced and compressed, with a fan-like arrangement of feathers; sternum well developed; ribs with uncinate processes; neck ribs joined to vertebrae.

Superorder Odontognathae. Ancient toothed birds from the Cretaceous period; sternum keeled or flat. (Fig. 34) *Hesperornis regalis*,* *Ichthyornis dispar*.*

Superorder Palaeognathae. Walking birds, flightless; many of large size; sternum flat; wings rudimentary; coracoid and scapula small and ankylosed; tail vertebrae free; no furcula; feathers usually hair-like. Examples: (Fig. 35) ostriches, rheas, cassowaries, tinamous, kiwi (*Apteryx*), Moas,* and *Aepyornis*.* Commonly called ratites.

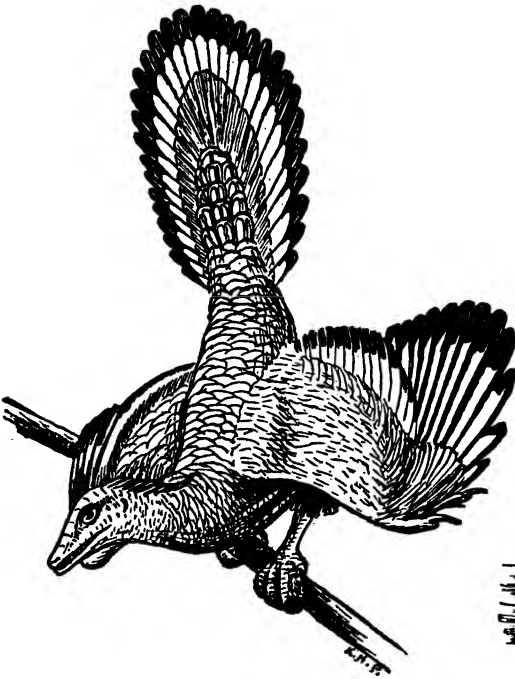


FIG. 33. *Archaeopteryx*.

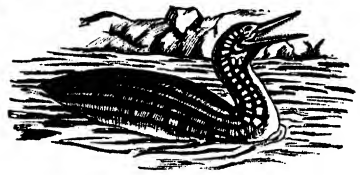
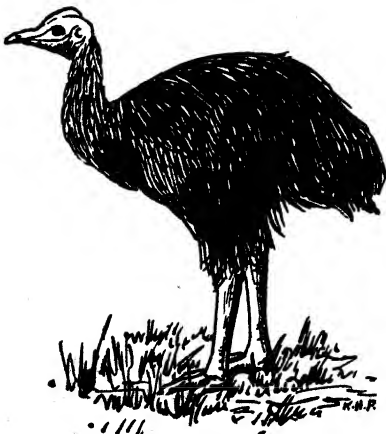


FIG. 34. *Hesperornis*.



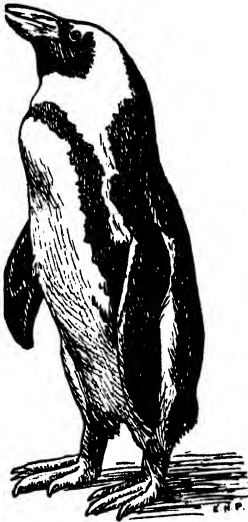
Cassowary



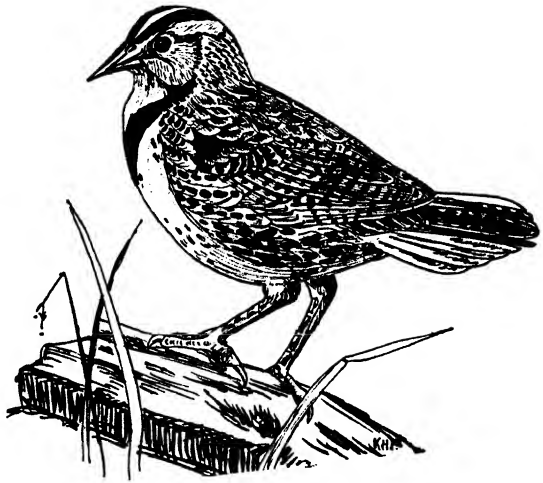
Kiwi, *Apteryx*

FIG. 35.

Superorder *Neognathae*. Modern birds with a keeled sternum (that is, all modern birds not in the *Palaegathae*); tail vertebrae five or six; fore limb with metacarpals joined and fingers included in the specialized wing; tarsometatarsus and carpometacarpus completely formed. (Fig. 36.) Commonly called carinates.



Penguin



Meadowlark

FIG. 36.

Mammals

Although the first known fossils of primitive mammals are from the Jurassic period, some of the small theromorph reptiles of the Permian and Triassic had many of the characters that were to be utilized in the new mammalian group. Their skeletons were becoming more refined without becoming overspecialized and without losing any of the essential structures for further developments. The brain was enlarging, the growth of the cerebral lobes being foreshadowed by an increase in the size of the pallium. The teeth, instead of being cone-shaped, could now be differentiated into incisors, canines, and molars. The jaws and ears were undergoing modifications that suggested what was to follow later, since the posterior part of the jaw was becoming small and weak, most of the stress being taken by the dentary and its processes. This was to leave the posterior end of the jaw free and in a position to be taken into the ear, along with the reduced quadrate, to form the mammalian incus and malleus. The articular was also greatly diminished

and was moved to the inside of the jaw. The squamosal was enlarged, being extended downward to form the new articulation for the dentary.

Primitive mammals continued to develop through the Mesozoic period, although their remains are few and their numbers small. At this time they were in competition with the great reptiles, and their progress was slow at best. With the advent of the Tertiary period, when conditions changed, the reptilian groups became greatly reduced or died out altogether and this was the opportunity for the newly developed mammals. They increased in numbers, and by the middle of the Tertiary most of the modern orders were differentiated and became somewhat similar to their present-day descendants. This was a period of further refinement, when the best seemed to survive, replacing the animals that were not able to meet the changing conditions and climate. Many grotesque forms arose but did not survive. Migrations were common, and there was an interchange of species and groups from continent to continent. During the Pleistocene period there was a general reduction in the abundance of practically all orders of mammals. The history of such groups, as the horse, camel, rhinoceros, and elephant, has been very completely reconstructed, so that the development of limbs, teeth, tusks, brain case, and other skeletal parts can be followed from their first appearance to their mature form. This has been of inestimable value in determining the exact way in which modern structures have been produced.

This hemisphere has had a most interesting history of mammalian development, evolution, and migration, but this is too large a subject to be included in a textbook. For a history of the mammals, the student is referred to detailed works such as Scott's "A History of the Land Mammals of the Western Hemisphere." Mammalian remains are found in practically every part of the United States. They are particularly plentiful in certain sections, such as the Bad Lands of South Dakota, northeastern Colorado, and western Nebraska. In one region of northern Colorado it is possible to walk for a half mile on a pavement made up of the bones of one of the Titanotheres, a large plains animal of the Tertiary period. Many of the states are strewn with elephant remains, both those of the mammoth and the mastodon. The Pleistocene period left thousands of these animals scattered over large areas, and it is safe to assert that, in many of the east central states, parts or whole elephants may be found in every square mile of large areas.

Mammals parallel the reptiles in their responses to the variable conditions of land life. They become differentiated into forms suited to changing environments and to various kinds of activities, such as walking, running, jumping, flying, climbing, digging, and swimming,

with a further division into carnivorous and herbivorous types, each with its special adaptations. The walking animals are those without any special adaptations of the limbs, either in skeleton or in musculature, and, although they are able to run, walking is their ordinary gait. The running forms are specialized in both skeleton and musculature, with every segment of the limbs elongated and with muscles suitable for active movements. Jumping animals include the kangaroos and the jumping mice and rats, with small fore limbs and greatly enlarged posterior limbs. Arboreal animals are found in many orders. The highest type is the gibbon, with its grasping hands and feet and elongated arms, though many other primates also live in trees. Sharp claws instead of grasping hands and feet are used by many other arboreal animals. Volplaning appears in *Galeopithecus* (Fig. 41), the phalangers, flying squirrels, and others. Strong claws and a special development of the skeleton and musculature of the fore limb enable some to become diggers. The ground is the home of many mammals that use it for protection and safety, and a few, such as moles or gophers, are real subterranean forms, getting their food and spending most of their time under the ground. The cetaceans, including the whales, dolphins (Fig. 46), and porpoises, are the most highly specialized for a water existence, and they need not go to land at any time. Another large series, including the seals, walruses (and sea-cows), live near the shore and depend upon the land for certain phases of their activities, such as the rearing of young. A large number of inland animals find the water very attractive and get most of their food along the lakes and water courses. Some of them, such as beavers and muskrats, cannot exist without a water environment.

With the great increase and spread of man in modern times, the larger mammals have been driven back to the frontiers, except those that have been domesticated and those for which large areas have been set aside under government control and protection. The smaller mammals are better able to continue in spite of man, but even they are becoming restricted, as their natural habitats are changed by continual tilling of the land, draining the swamps, changing the water courses, cutting the timber, over-grazing, and the building of dams. The fate of the mammals rests largely in the hands of man, and the future is doubtful.

General Characteristics of Mammals

The mammals are distinguished from other vertebrates by the number of characters. Hair is the characteristic epidermal covering on all mammals, although it may be vestigial as in the whales and *Sirenia* (Fig. 48). Scales and bony plates are present in only a few mammals. The mammary glands are

unique and supply milk for all young. Sweat and oil glands may be present in the skin, which is thicker than in other vertebrates and has a better-defined epidermal layer of living and dead cells.

The heart is four-chambered as in birds, but the left half of the aortic arch, instead of the right, becomes the systemic vessel. The red blood corpuscles are small and without nuclei. A complete muscular diaphragm separates the lungs from the peritoneal cavity. The brain is larger in proportion to the body weight and is marked by new structures that did not appear in the lower groups. The cerebrum is enlarged; the pallium is much thickened, and the greatly enlarged cerebrum covers most of the rest of the brain. In the higher animals, the right and left lobes of the cerebrum are connected by the corpus callosum, a heavy set of commissures. The optic lobes, which appear in lower vertebrates as a pair of lobes called the corpora bigemina, appear to be divided transversely to form the corpora quadrigemina in the mammals. The cerebrum adds a pair of lateral lobes connected by a new commissure, the pons. The eyes with elliptical lenses are capable of focusing for widely different ranges of vision. The ear is different from that of all other vertebrates in that three ossicles are present in the middle chamber. There is a marked specialization of the lagena to form a coiled cochlea with its organ of Corti.

No cloaca is present in the higher mammals. The lungs are sponge-like and lie in pleural sacs, separated from the body cavity by the diaphragm, which assists the intercostal and abdominal muscles in inhalation and exhalation. The larynx has an additional cartilage, the thyroid, and vocal cords are stretched from the thyroid to the arytenoids, forming sound-producing structures. The epiglottis, a new structure, forms a flap over the entrance to the glottis.

The teeth are typically differentiated into incisors, canines, premolars, and molars, and usually the milk dentition is followed by a second or permanent set. Teeth are present only on the dentary, premaxillary, and maxillary bones. A hard palate, formed by the palatines and maxillae, separates the nasal cavity from the mouth, and nasal scrolls are highly developed. There is a reduction of the number of bones in the skull by fusion and some elimination. The temporal bone is formed by a fusion of a number of bones including the squamosal which supplies the articulation for the lower jaw, thus replacing the quadrate. The occipital condyles are paired as in amphibia. The quadrate and the articular move into the ear to form the incus and malleus, thus forming with the stapes the three ossicles. The jaw consists of paired dentaries, which may be ankylosed into a single structure or merely joined by a symphysis. The vertebral column is divided into definite regions. Usually only seven cervical vertebrae are present, the first two being highly modified into an atlas and an axis. The anterior girdle is reduced in all but the monotremes, which still possess a reptilian girdle. In the higher mammal the pectoral girdle is composed of the scapula and sometimes a clavicle. The coracoid has been reduced to a mere process on the scapula, and the pre-coracoid and interclavicle have disappeared.

The kidneys are rather compact metanephroi. The ureters empty into a urinary bladder and, as in the reptiles, carry no reproductive products. A urethra drains the bladder. A penis is present in the males. The testes may be inside the body cavity but often descend into a scrotal sac. The vas deferens or mesonephric duct carries the spermatozoa from the testes and

empties into the urethra. Numerous glands are associated with the male reproductive system to furnish a vehicle for the sperm. All female mammals except monotremes modify the oviduct into distinct regions: the vagina, the uterus which is paired but tends to fuse, and the Fallopian tubes receiving eggs from the ovaries. The ovaries and the ova are very small in all except the monotremes. Monotremes lay eggs, but all the other mammals give birth to living young. Marsupials, which have a very short period of gestation, give birth to very immature young. The placental mammals have a much longer period of gestation, and the developing young form a uterine attachment, the placenta, from their fetal membranes.

Classification of Mammals

Subclass PROTOTHERIA. Egg-laying mammals; mammary glands without teats; temperature variable; no placenta; shoulder with coracoid, precoracoid, and interclavicle; epipubic bones present, scapulae



FIG. 37.

without crests, brain of low type; have a cloaca. Only living order Monotremata, containing *Ornithorhynchus* (duckbill) and *Echidna* (spiny anteater), found in Australia and surrounding islands only. (Fig. 37.)

Subclass METATHERIA. Viviparous mammals; generally without a functional placenta; young born in immature stage; usually with a



FIG. 38.

marsupial pouch and epipubic bones; nipples developed to which the young attach while in the pouch; vagina often with a third diverticulum; palate usually fenestrated; angle of jaw inflected; distinct dental formula; brain of low type.

Order *Marsupialia*. Opossum, wombats, *Caenolestes*, kangaroos, phalangers, etc.

Subclass EUTHERIA. Mammals with a functional placenta; brain case comparatively large; brain with corpus callosum; typical dental formula $\frac{3-1-4-3}{3-1-4-3}$; no epipubic bones; young highly developed when born.

Order *Insectivora*. Usually small mammals with five digits all clawed; feet plantigrade; generally insect-eaters; teeth with many



Shrew



Mole

FIG. 39.

sharp points; canines slightly separated from incisors and pre-molars; brain small, with smooth hemispheres; with clavicles. Examples: (Fig. 39) shrews, moles, etc. Cosmopolitan.

Order *Chiroptera*. Small mammals with fore limbs modified for flight; insectivorous and herbivorous; large olecranon process; five digits with claws; tympanic ring formed. Examples: (Fig. 40) bats, all over the world.



FIG. 40. Bat.

Order *Dermoptera*. Small, clawed mammals with a fold of skin between the legs which acts as a parachute; herbivorous; pectoral teats; molars multicuspidate; peculiar comb-like lower incisors. Examples: (Fig. 41) flying lemur (*Galeopithecus*).

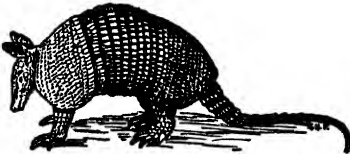
Order *Pholidota*. Medium-sized, clawed mammals covered with large epidermal scales and but few hairs; toothless; tongue worm-like; feet plantigrade. Examples: (Fig. 42) pangolin (*Manis*).



FIG. 41. *Galeopithecus*.



FIG. 42. *Manis*.



Armadillo



Sloth

FIG. 43.

Order *Xenarthra*. Large group of much-diversified edentates; tree-living, digging, and insectivorous; unguiculate; teeth, if present, are all of the simple peg-like type, without enamel and rootless; skin covered with hair, horny or bony scales; thoracic and lumbar vertebrae with extra accessory processes.

Examples: (Fig. 43) armadillo, sloth, anteaters, *Megatherium*. An enormous group in past times, during the Miocene period in South America.

Order *Rodentia*. Clawed mammals, usually of small size, with incisors specialized for gnawing; feet plantigrade or semiplantigrade; usually herbivorous but sometimes omnivorous; incisors shaped like a half circle, with open roots and a persistent growth; no canines; wide diastema, or space, between incisors and molar series; molars with a distinctive pattern, either bunodont or lophodont. It formerly contained the hares and rabbits as a suborder; properly contains rats, mice, squirrels, beaver, porcupine, and other rodents. The largest known rodent is a fossil beaver, *Castoroides*, an animal as large as a black bear, widely distributed



FIG. 44. Muskrat.

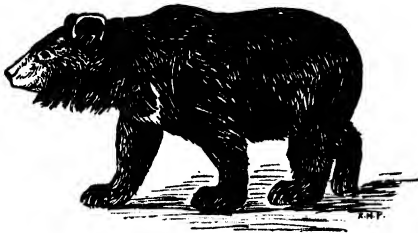
in North America during the Pleistocene period. The largest living rodent today is the Capybara of South America. Examples: Muridae (rats and mice), Sciuridae (squirrels), Castoridae (beaver), Erethizontidae (porcupines), Geomyidae (gophers), etc.

Order *Lagomorpha*. Dentition similar to that of rodents except an accessory pair of small upper incisors present back of the functional pair. Body plan quite different in many details from that of the rodents. Examples: Leporidae (hares and rabbits), Ochotonidae (conies or pikas).

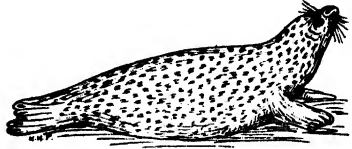
Order *Carnivora*. Unguiculate, flesh-eating mammals with small incisors and large canines; anterior molars or premolars usually modified for shearing; clavicle rudimentary or lacking; divided into two suborders: the Fissipedia, living on land, comprise the Viverridae (genets), Felidae (cats), Hyaenidae (hyenas), Canidae (dogs and wolves), Mustelidae (weasels), Procyonidae (raccoons), Ursidae (bears); the Pinnipedia, living in water, with limbs modi-

fied to form paddles or flippers, comprise the Phocidae (seals), Otariidae (sea-lions), and Odobenidae (walrus). (Fig. 45.)

Order *Cetacea*. Sea-mammals with cylindrical bodies and smooth glandless skins; tail fin horizontal; nasal openings far back on



Bear



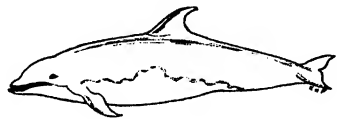
Seal

FIG. 45.

the skull roof; teeth peg-like if present; anterior limbs flipper-like with skeletal parts much modified; posterior limbs missing, with a few pelvic parts persisting as rudiments; adipose azygous fins. Examples: (Fig. 46) *Balaenopteridae* (whales), *Delphinidae* dugong (*Halicoridae*), manatee (*Manatidae*).

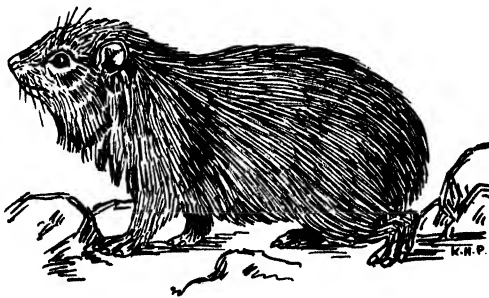


Whale



Porpoise

FIG. 46.

FIG. 47. *Hyrax*.

Order *Hyracoidea*. A small group of plantigrade-herbivorous ungulates with hoofs; premolars and molars lophodont, four toes on anterior limbs and three on the posterior limbs. Example: (Fig. 47) *Hyracidae* (cony) of Asia.

Order *Proboscidea*. Five-toed, herbivorous mammals with upper lip and nose converted into a trunk; second incisors modified into tusks; molars lophodont or bunodont; canines missing; limbs straight. Examples: Elephantidae (elephants) (mastodons and mammoths in the past).

Order *Sirenia*. Herbivorous ungulates living in the sea, with anterior limbs paddle-like and posterior limbs missing; pelvic bones vestigial; teeth lophodont. Examples: (Fig. 48) sea-cows, dugong (*Halicoridae*), manatee (*Manatidae*).

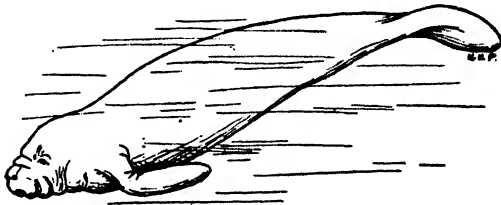


FIG. 48. Manatee

Order *Artiodactyla*. Herbivorous ungulates, living mostly on land, with the axis of the foot between toes 3 and 4; toes 2-4 in modern forms; incisors and canines of upper jaw often missing; teeth bunodont, buno-selenodont, or selenodont; stomach sometimes complex. Examples: (Fig. 49) Bovidae (cattle), Cervidae (deer, musk deer, sheep), Suidae (pig), Hippopotamidae (hippopotamus), Giraffidae (giraffe, and Camelidae (camel).



Antelope



Hippopotamus



FIG. 49.

Order *Perissodactyla*. Herbivorous, land-living ungulates with axis of foot through toe 3; toes odd in number; incisors $\frac{3}{3}$; molars $\frac{3}{3}$.

lophodont or selenodont; no gall bladder. Examples: (Fig. 50) Equidae (horses, asses, zebra), Tapiridae (tapir), and Rhinocerotidae (rhinoceros). (Fig. 51.)

Order *Tubulidentata*. Plantigrade anteaters of Africa; claws greatly elongated; teeth enamelless and rootless. Example: (Fig. 52) *Orycteropodidae* (aardvark or *Orycteropus*).

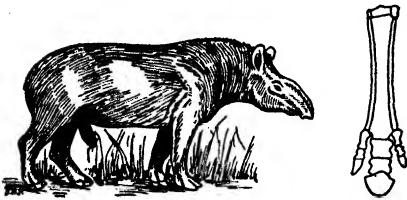


FIG. 50. Tapir.

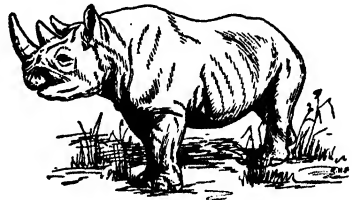


FIG. 51. Rhinoceros.

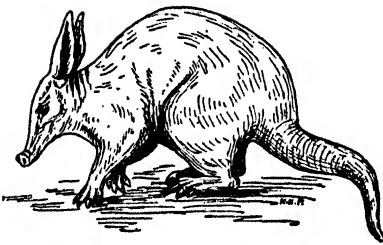
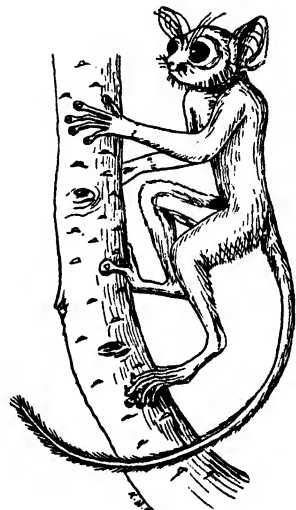
FIG. 52. *Orycteropus*.

FIG. 53. Lemur.

FIG. 54. *Tarsius*.

Order *Primates*. Plantigrade, omnivorous mammals; usually with nails; orbits surrounded by a bony ring; pollux and hallux opposable; brain case usually large; molars quadritubercular or quintitubercular; incisors $\frac{2}{2}$.

Suborder Lemuroidea. Low primates in which the brain case is small and the brain simple; nose elongate; arboreal; many nocturnal; inner incisors of upper jaws usually separated. Example: (Fig. 53) Lemuridae (lemurs), etc.

Suborder Tarsioidea. Small group of one genus; with a dentition of $\frac{2-1-3-3}{1-1-3-3}$; orbit separated by a bony partition from the temporal fossa. Example: (Fig. 54) Tarsiidae (*Tarsius*).

Suborder Anthropoidea. Brain much convoluted and the cerebral lobes cover much of the cerebellum; mammae always pectoral; inner pair of incisors of upper jaw in contact. Examples: Hapalidae (marmosets), Cebidae (howling monkeys), Cercopithecidae (baboons, and monkeys of the catarrhine group), Hylobatidae (gibbons), and Anthropoidea (orang, chimpanzee, gorilla, man).

CHAPTER FIVE

Embryology

In order to understand the homologies of vertebrate structures it is necessary to understand their general embryological origin. Each system is developed from a rather definite basic plan common to all vertebrates. The differences in structures characteristic of the different groups of vertebrates are due largely to the extent and the manner in which the various parts of the basic plan are developed. Vertebrates differ not so much through alterations of the basic plan as through alteration of the method of development after the basic plan is formed. They may neglect to develop certain parts and develop other parts of the basic systems. An important basis for an understanding of comparative anatomy lies in a knowledge of the fundamental principles of vertebrate embryology.

The study of the development of animals has greatly enriched the field of vertebrate zoölogy, since it has answered many questions in morphology that could have been answered in no other way. The impetus given to developmental studies by the evolution idea served to stimulate a large number of workers who were seeking to learn something of phylogeny and the mysteries of evolution through this tool. In one sense, the results have been disappointing, since many of the events occurring in the embryological development of the individual can hardly be considered a part of the actual history of the species. The telescoping and transposition of the changes, with a reversal of sequence in some cases, caused many misinterpretations of embryological stages. Many phenomena observed in the embryo represent nothing but developmental needs and have no evolutionary significance whatsoever. The embryo is developed under conditions that are hardly to be compared with adult surroundings, and, as would be expected, the embryo must solve its problems in its own way. Many conditions and structures met with in the embryo must be considered in their proper relations, and it is not always necessary that these structures have any relation to the past, present, or future development, but may be considered as purely embryonic adaptations. At one time, embryonic speculations were all interpreted as an indication of a part of the

evolutionary history, but many of these assumptions have been discarded as untenable. There is, however, a certain similarity in development that extends throughout the vertebrates, and here, ontogeny and phylogeny have a proper place.

Any organ or system may be studied in development, and the exact sequence of its changes registered. In these studies, much valuable knowledge has been gained that may be used in determining the origin of some of the anatomical parts and their relation to the past ages.

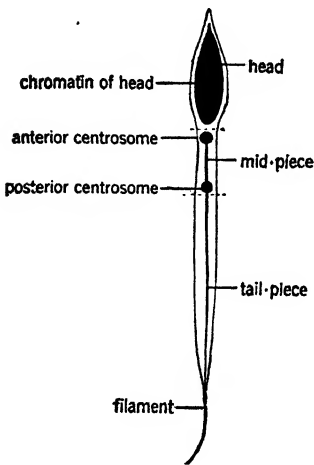


FIG. 55. Spermatozoön. After Jenkinson.

The embryological study of the chondrocranium, ear ossicles, the excretory, circulatory, and nervous systems, and other structures has added much that has been of value in clearing up origins. This study of the embryological history of parts has filled in many facts that would have remained unknown or problematical, if interpreted only from adult conditions.

Ovum and Spermatozoön

The development of every vertebrate starts with the fertilized egg, derived from an egg and a sperm. The ovum, or egg (Fig. 299), is a specially developed body cell from a region set aside early in the development of the embryo. These cells migrate into position in the region that is going to be the ovary and form the basis for future egg development in the animal. The primordial eggs undergo a number of divisions until finally some of these become functional eggs. The egg is distinguished by its large size, since it generally carries food, and by its lack of ability to move. In the divisions of the egg the process of maturation cuts the chromosome number in half, and only one of the four cells formed by the maturation division becomes functional, the others being cast aside as polar bodies. The egg consists of the heredity-bearing bodies—the chromosomes—cytoplasm, food material, together with shell and membranes, where these are present. There is a direct relation between the food material and the way in which the egg develops. Since mammals of the placental type carry little food yolk, the eggs are very small (one-fifth of a millimeter in man).

The spermatozoa (Fig. 55) are developed in the testes, to which the primordial germ cells migrate in the development of the embryo. A spermatozoön differs from an ovum in being much smaller and of a more complicated structure, in being motile, and in carrying no

food material. In the maturation process all the resulting cells become functional. The typical spermatozoön consists of a head, which contains the hereditary material, a mid-piece, an accessory structure, and the motile tail. The tail part enables the spermatozoön to swim in water or to travel over the moist membranes of the female reproductive tubes until the egg is reached. Fertilization generally takes place in the upper end of the oviduct or in the water.

General Points concerning Vertebrate Eggs

Throughout the vertebrates, development is by means of a fertilized egg, but the treatment of the egg varies greatly in the different classes. The more common condition consists of the development of an egg that is supplied with sufficient food to carry it through its developmental stages, so that it is able to care for itself. This type of egg may be fertilized either before or after it is laid. In lower forms it receives no parental care and must depend upon the surrounding medium for proper hatching conditions. The term oviparous is applied to egg-laying animals.

The opposite extreme is the viviparous type in which the egg is retained in the body of the parent until it has undergone part or all of its development. The viviparous condition varies from that in which the eggs are retained in the body, receiving no nourishment from the mother, to that in which all the food material is transferred to the embryo through a placenta. The term ovoviviparous is applied to animals in which the eggs are retained in the oviduct until hatched, but this condition intergrades with the strictly viviparous condition, so that its meaning is not clear. In all classes except birds, groups are found in which some provision is made for the transfer of additional food to the young, either through an omphaloplacenta or through an allantoic placenta, or both. Since the amnion and allantois are not present in fishes and amphibians, other means must be developed for the transfer of food in the viviparous species, and generally this is the development of the omphalo-, or yolk-sac, placenta.

The eggs of the fishes vary greatly in size, those of the Elasmobranchii being the largest and those of the Teleostei the smallest. Fishes laying large eggs have a small number (10 to 20), but some of the teleosts (cod) lay more than a million. The young are provided with a supply of food which is contained in a yolk-sac, and this must be sufficient to carry them through their entire development. An early development of the heart and circulatory system supplies the embryo with means of distributing the food to different parts of the body and also provides the means for getting oxygen and removing waste. Whereas in most cases the egg is merely retained in the oviduct,

in a few species an omphaloidean placenta is formed, which comes in contact with the uterine wall and is able to transmit food from the mother to the young and possibly to remove waste. *Mustelus laevis* and *Carcharias* of the Elasmobranchii have this yolk-sac placenta. *Pteroplatea micrura*, a ray, develops peculiar long villi in the walls of the uterus which enter the spiracle of the embryo and extend down into the esophagus, probably assisting in respiration and possibly in a transfer of food material. The bitterling, *Rhodeus amarus*, places its eggs in the gills of clams, where they burrow, living parasitically until they are ready to care for themselves. The sea-horses have a small marsupium which develops on the ventral side anterior to the pelvic fins, and in this the eggs are received and carried through development. Some of the catfishes carry the eggs in the mouth and gill chamber until they are hatched, and the young may return there for safety after hatching.

Practically all the amphibia are oviparous, and in addition most of them lay their eggs in water because of the metamorphic changes which make water necessary in the development of the young. The eggs carry some yolk but not a great amount and are surrounded by a jelly-like material which absorbs water when the eggs are laid. This is a sterile material which supplies some food and protects the young. There are some peculiar means of caring for the young. The European obstetric male toad fertilizes the eggs as they are laid and, wrapping them around his legs, keeps them there until they are hatched. The South American toad, *Pipa americana*, develops a series of pits in the skin of the back at breeding time, and in these pits the eggs sink and remain during all the developmental stages. *Rhinoderma darwini* carries the eggs in the vocal sac, retaining them until after metamorphosis of the developing young. Some amphibians that live on rocks and trees lay their eggs in damp earth or leaves, covering them with a foamy material which preserves the moisture. These have a very short metamorphic period. *Ichthyophis glutinosa* coils around its eggs in its underground burrow. *Salamandra atra*, a European form, is the only known amphibian in which ovoviviparity is approached. Its young seem to be reduced in number by cannibalism within the uterus, and only those that survive this uterine struggle are born. No shelled eggs occur in the Amphibia of the present day, and this is peculiar, since in every other class shelled eggs are laid by some of its members.

The embryos of reptiles, birds, and mammals have two new membranes, the amnion and allantois (Figs. 56, 57). The amnion surrounds the embryo and forms a liquor-filled protecting chamber; the allantois spreads over the embryo and is an organ of respiration and excretion. Both these membranes are developed by the embryos themselves.

Some reptiles are oviparous and others ovoviviparous, but egg-laying, is the more common. The egg-laying forms may have a hard-shelled egg, as in the alligator, or it may be soft and leathery as in the snakes. The eggs are usually of comparatively large size and well supplied with food material. In *Phrynosoma*, the horned toad, both types of development

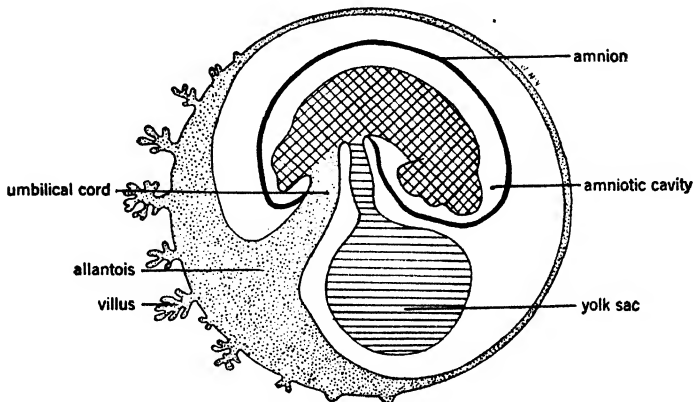


FIG. 56. Embryonic membranes of developing placental. After Weber.

are found in the same genus, since some lay eggs and others retain them and bear living young. Among the snakes, numerous groups are ovoviviparous, including the crotaline snakes, the gartersnakes, and some other water snakes. Two snakes have been found with an allanto-placenta, in which there is an evident transfer of materials from the

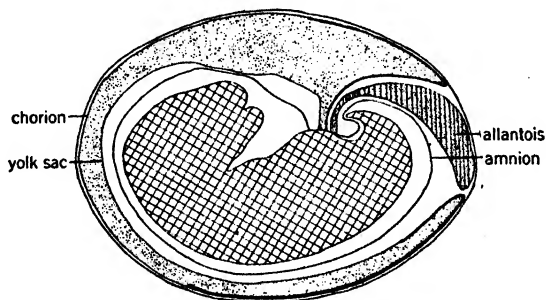


FIG. 57. Embryonic membranes of a developing marsupial. After Weber.

mother to the young (*Denisonia suta* and *Denisonia superba*). It has long been known that the lizard, *Chalcides tridactylus*, developed both an omphalo- and an allanto-placenta, and Weekes (1929) found the same character in an Australian lizard of the genus *Lygosoma*. The strictly water reptiles, such as the sea-turtles and the fossil ichthyosaurs, had either to develop living young or come to land at egg-laying

time. The turtle still comes to the sands of the shore to lay its eggs, but the fossil ichthyosaurs have been found with young in the body cavity, establishing the fact that they were ovoviviparous, with the possibility that some maternal connection was formed. The young were evidently born in the water, which is rather unusual for a reptile.

The eggs of birds are covered with a hard shell, and development is the same throughout the group. There is considerable difference, however, in the amount of food that is supplied, and for this reason eggs are large or small in proportion to the parental weight. The large eggs, with abundant food material, are able to carry the young to a stage where they are almost self-sustaining from the time of hatching; the smaller eggs have so little food material that the young are hatched in an immature condition, with no feathers and with closed eyes. The number of eggs varies from one to twenty or more, and with few exceptions they receive parental care. The cowbirds (*Molothrus*) deposit their eggs in other birds' nests, and the Australian brush turkey makes a large mound of leaves, in which the eggs are deposited and left to shift for themselves. The penguin carries its single egg in an improvised marsupium between its legs.

The mammals differ from the other amniotes in that there is a reduction of the amount of food in the yolk-sac, and means of obtaining nourishment are provided by the placenta and later by the mammary glands only. The monotremes lay eggs with large yolks, which resemble those of birds and reptiles and develop in much the same way, but the young, when hatched, obtain food from the mammary area of the mother. The marsupials retain the egg, but the gestation period is for only a few weeks so that there is little differentiation of the placenta. The young are born when very immature and complete their development in the marsupial pouch, supplied with food by the mammary glands. The allantois, in general, serves as an organ of respiration and excretion and in most marsupials never comes in contact with the wall of the uterus (Fig. 57), but in a few there is a temporary contact, and in *Perameles* a definite placenta is formed. The yolk-sac is quite large in the marsupials and surrounds the embryo, so that the allantois cannot reach through the chorion to the wall of the uterus. In placental mammals the placenta is perfected so that it transfers food materials from the mother to the embryo (Fig. 56). With the changed function of the allantois, the yolk-sac becomes reduced in size and serves no important function in nourishing the embryo. The placenta is quite variable, both in actual shape and in its connection with the wall of the uterus. The allantois comes in contact with the chorion, which in turn makes a contact with the wall of the uterus through the development of villi (Fig. 56).

If there is no intimate growing together of the uterus and placenta, at birth the placenta pulls away free from the maternal tissues. The deciduate type forms an intimate connection with the wall of the uterus, and at birth a part of the uterine wall separates off and is shed with the placenta. The shape of the placenta varies from the primitive type in which the chorion (Fig. 57) is completely covered with villi to that in which the villous areas are restricted to form cotyledons (in sheep), a band around the embryo (in most carnivores), or a disc-shaped placenta (in man).

Fertilization

All vertebrates start from a zygote formed by a spermatozoön and an egg, each a product of the gonads. The sex cells are of course directly continuous in their history with other cells of the body, but their differentiation appears to come early in the life of the animal. The eggs are always large in comparison to the spermatozoa, generally carry food material, and are non-motile. The spermatozoa are extremely small, carry no food material, and are motile. In internal fertilization the spermatozoa ascend the oviduct until the egg is reached. Eggs externally fertilized usually have the spermatozoa shed over them. There is probably a chemical action or attraction that accounts for the finding and penetration of the egg by the spermatozoa.

Cleavage

When the egg and the spermatozoön unite, they form the unit from which the new animal is to be developed, namely, the zygote, or fertilized egg. The zygote immediately begins to divide, thus forming a number of cells, or blastomeres. This is known as cleavage, and the cleavage type depends largely on the amount of yolk present. This division of the zygote into blastomeres is a perfectly regular process in eggs with little or no yolk, but becomes irregular when the egg is loaded with food, because the yolk-laden blastomeres cannot keep up with the rapidity of division of those which have little food (Fig. 58).

Since most vertebrates have eggs with large amounts of yolk, the cleavage pattern and resulting gastrulation are often greatly modified. The general plan of early embryological development can be seen most clearly in the development of an egg possessing very little yolk. Mammalian eggs with little yolk still follow a highly modified pattern, probably inherited from their large-yolked ancestors. The clearest pattern of development can be seen in the pre-vertebrate *Amphioxus*, where little yolk is present to modify the general plan. Consequently for a brief description of the stages of embryology within the scope of this book, the early stages of the development of *Amphioxus* will

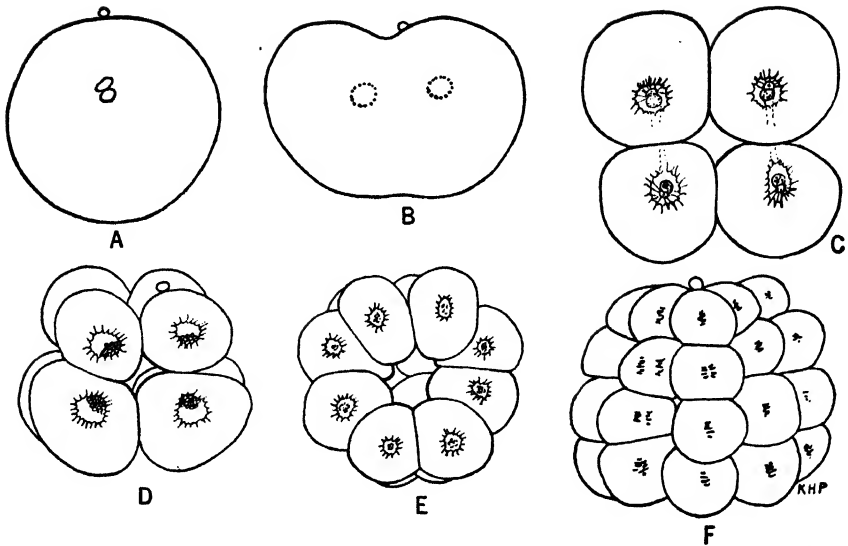


FIG. 58. Cleavage of the *Amphioxus* egg. After Shumway. A, fertilized egg or zygote; B, dividing into two cells; C, four-celled stage; D, eight-celled stage; E, sixteen-celled stage; F, thirty-two celled stage.

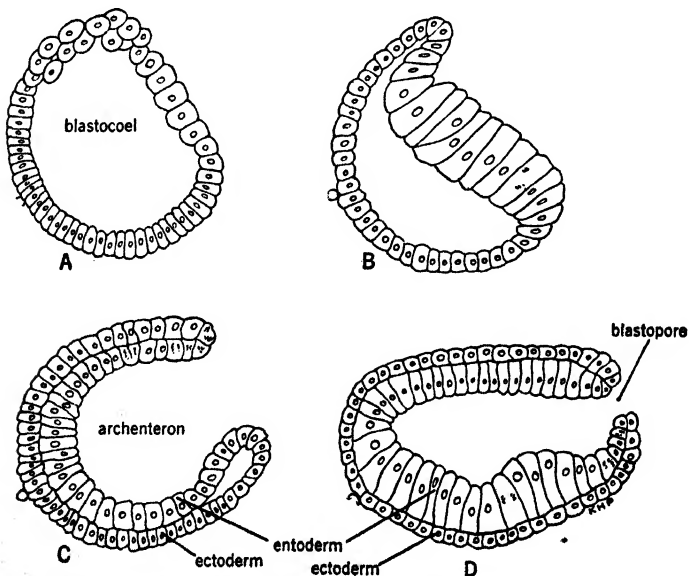


FIG. 59. Developing *Amphioxus*. From Wieman, after Cerfontaine. A, blastula with flattened vegetative pole; B, invagination of the yolk laden cells; C, gastrula formed; D, completed gastrula.

serve better to illustrate the early embryology and the formation of the general basic plan of a vertebrate than that of any single vertebrate.

The first division of the egg is polar, dividing the zygote into two blastomeres; and the second is at right angles to the first, forming four. The third division is equatorial, forming eight blastomeres, and is followed by two more divisions between the equator and the poles, thus forming sixteen cells. Rapid divisions follow until the cells finally arrange themselves so as to form a hollow ball, the blastula, with its segmentation cavity (Fig. 58).

Gastrulation

In this blastula (Fig. 59), the lighter cells bearing no food are at the apical pole, and the heavier, food-laden cells are at the opposite pole, thus differentiating the two. By a process known as gastrulation, which

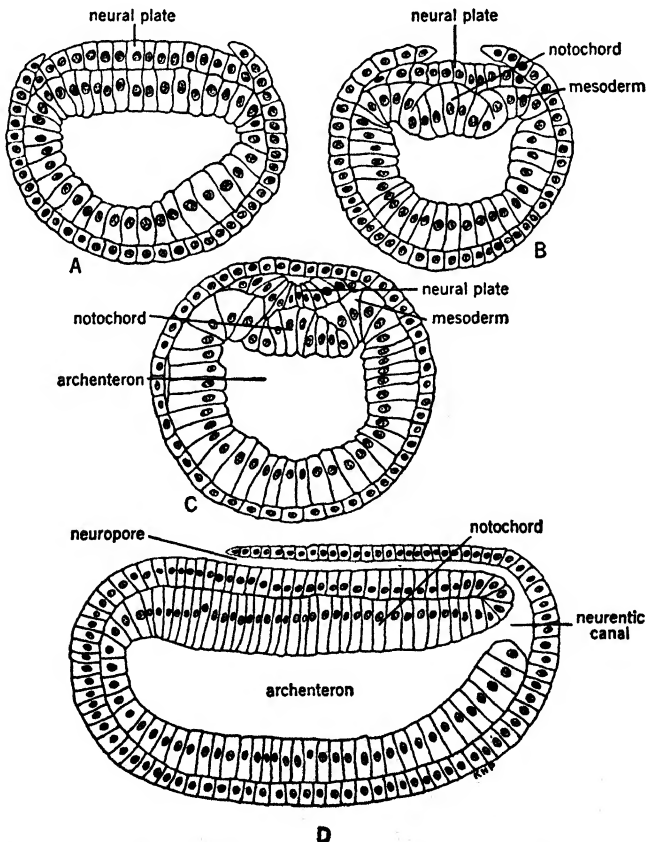


FIG. 60. Cross and longitudinal sections of developing *Amphioxus* to show differentiation of layers and parts. From Wieman, after Cerfontaine.

varies in different forms, a two-layered structure, the gastrula, is obtained, the inner layer of which is made up of food-bearing cells and the outer layer of cells not containing food. Of the two layers so formed, the outer becomes the ectoderm and the inner the endoderm. The opening of the gastrula, or blastopore, is quite distinctive in the eggs of lower vertebrates. The gastrula (Figs. 59, 60, 61), develops rapidly and assumes polarity so that there is an oral and aboral end.

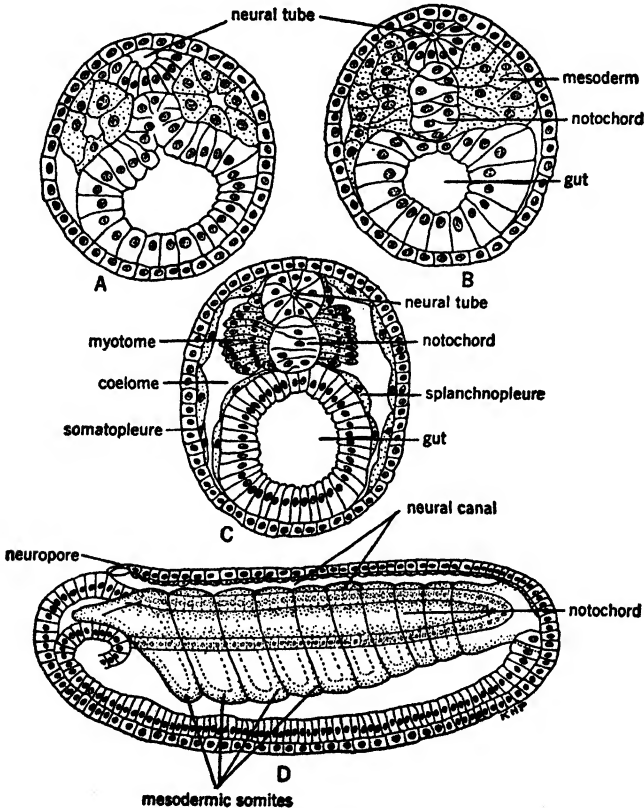


FIG. 61. Sections of developing *Amphioxus* to show development of primary parts. A, B, C, cross-sections; D, sagittal section. From Wieman, after Cerfontaine.

Mesoderm Formation

With continued development, a third layer, the mesoderm, is formed. This begins at the oral end with coelomic pouches that appear in the sides of the entoderm. These continue to grow and develop a cavity which is to be the coelom. A number of pouches develop in the head, only to disappear, but the others gradually enlarge and eventually cut loose from the parent tissue, thus forming the metameric, mesodermic

somites. In true vertebrates, mesoderm originates by various ways other than from the entoderm, but many believe that this enterocoelous mode is ancestral. The pouches become differentiated into three regions, a dorsal epimere, a median mesomere, and a ventral hypomere, each forming its part of the growing animal.

The epimere becomes differentiated into several regions: the dermatome, to form the corium of the skin; a sclerotome, to form the axial skeleton; and a myotome proper, to form the epaxial and hypaxial musculature. The mesoderm of the epimere grows ventrally, forming the musculature of the body wall from its inner portion and the corium of the skin from its outer (Fig. 62).

From the mesomere are formed the organs of excretion and reproduction, together with their ducts, and parts of the circulatory system. The hypomere, which consists of two sac-like extensions along the side of the gut, eventually grows ventrally to fuse beneath the mesomere, thus forming the coelomic cavity. The inner layer covering the gut forms the mesenteries and visceral peritoneum, while the outer layer becomes the inner lining of the body wall.

The mesenchyme, formed from cells of mesoderm and probably also from ectoderm and endoderm, is made up of scattered irregular cells, which pack in around structures, thus filling all spaces that are eventually to be connective tissue.

The endoderm continues to serve as the lining of the digestive tube, also lining all structures that are formed as diverticula, such as the liver, pancreas, and lungs. In an early stage in *Amphioxus* a ridge appears on the dorsal side of the gastrocoele which is pinched off to become the notochord. Since this occurs at the same time that the mesodermal pouches are formed, there is some question as to whether the notochord is endodermal or mesodermal. In the true vertebrates, the notochord arises simultaneously with the mesoderm, and it is impossible to assign it to any particular germ layer. The ectoderm and mesoderm are called upon to form a great variety of structures.

Derivatives of the different layers are summarized below:

(1) Ectodermal derivatives:

Outer layer of the skin.

Linings of the mouth, anus, and nasal passage.

Epidermal coverings such as horny scales, hair, feathers, horns, nails, spurs, enamel of teeth and of scales.

The nervous system entire, including sensory part of the eye, nose, ear.

(2) Mesodermal derivatives:

Skeletal parts and muscles. Bony scales, and dentine.

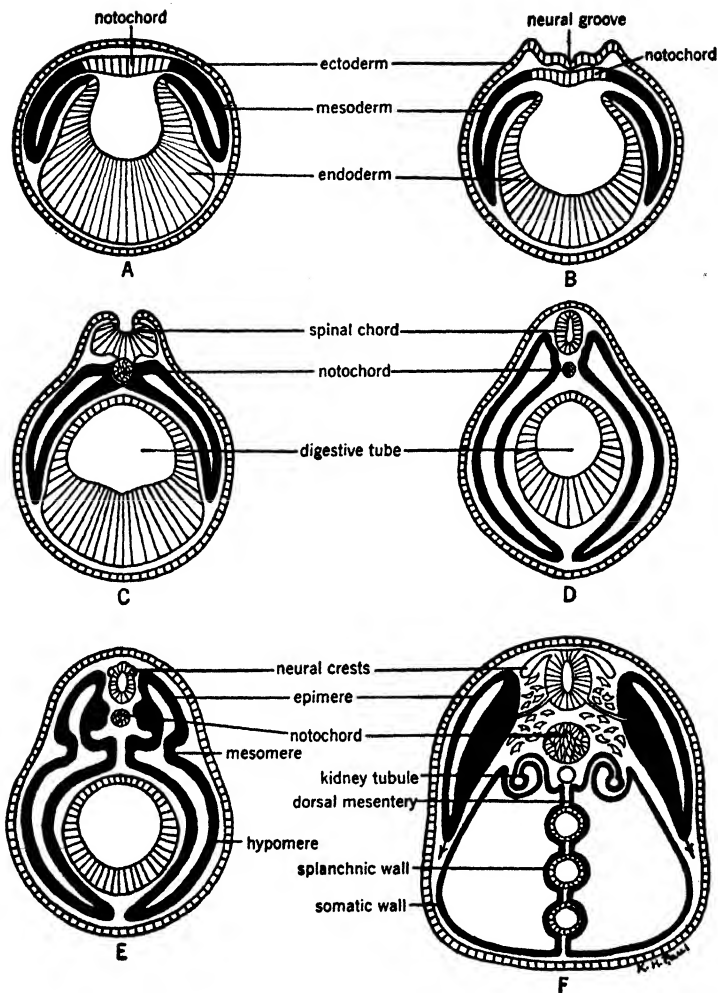


FIG. 62. Diagrammatic cross-section of anterior end of a generalized vertebrate embryo to show the relations of the germ layers. *A*, early stage showing the origin of the mesodermic pouches; *B*, early stage showing the neural groove, neural ridge, notochord, and growing mesodermic pouches; *C*, stage in which the neural infolding is almost complete, and the mesodermic pouches are separated from the other tissues, and somewhat extended ventrally; *D*, neural tube separate from the ectoderm, mesodermic pouches further extended; *E*, advanced stage in which the neural crests are beginning to show, the mesoderm is dividing into three regions, the epimere, mesomere and hypomere. Mesoderm greatly extended to surround the whole body; *F*, epimere is cut away from the rest of the mesoderm and starts a ventral extension that stops at the linea alba. The mesomere is developing to form the kidneys and gonads, while the hypomere is surrounding the digestive tube, forming the splanchnic sections which form the mesenteries and the serosa of the digestive tube; and the somatic layer which lines the coelomic cavity. The mesenchyme cells surrounding the neural tube and the notochord are forming the vertebrae.

Organs of excretion and reproduction.

Supporting materials such as cartilage, connective tissue, ligaments, tendons, and notochord of some vertebrates.

Circulatory system, including heart and vessels (lining in doubt).

Lining of the coelomic cavity.

(3) Endodermal derivatives:

Primarily the lining of the digestive tube and its derivatives, including the thymus and thyroid, lung ducts and secretory parts of liver and pancreas.

The specificity of the germ layers suggested is not absolutely rigid, since most organs are composite in their origin, being derived from two or three germ layers. Thus the stomach, lungs, tongue, and many other organs are composed of tissues from more than one of the primitive germ layers.

Germinal Disc

The development of the germinal disc shows a series of events that have a similar aspect in all vertebrates. The disc is the active area of protoplasm, on top of the yolk in eggs with a large yolk. Owing to the large amount of yolk, cleavage may only occur within the disc. In small eggs, with little or no yolk, early cleavage results in divisions through the yolk. From the dorsal surface the germinal disc shows ridges and a median groove that is the start of the nervous system. A rapid proliferation of cells changes the groove into a tube, completing the closure, and thus forming the embryonic brain and spinal cord. Beneath this activity of the surface, the other tissues are differentiating and the newly formed mesoderm is seen as tiny blocks along the side of the neural tube. Still deeper, the circulatory system is being laid down, and, with a rapid growth of the blood vessels over the yolk, a food supply is readily available and the possibility of removing waste is set up.

It is possible to present but little in an introduction, since this is an extremely large field of zoölogy and should be studied in textbooks devoted to embryology.

Development of Systems and Organs

Nervous System

The nervous system (Figs. 60, 61) is first considered because it is among the first to form and much of the early development is visible without sectioning. After gastrulation, there is a thickening along the future dorsal surface, and a medullary plate appears as a raised struc-

ture that is elongated and elevated above the rest of the surface of the ectoderm. In cross-section, this part becomes a deeper and deeper groove, until it is finally roofed over, forming a hollow tube, enlarged at the anterior end for the future brain, the posterior part becoming the spinal cord. The enclosed cavity becomes the lumen of the cord and the ventricles of the brain. From the walls of this tube, the nerve cells and the nerves take origin. The ectodermal nervous system is now sunken below the rest of the body. Thus, what was the covering of the body

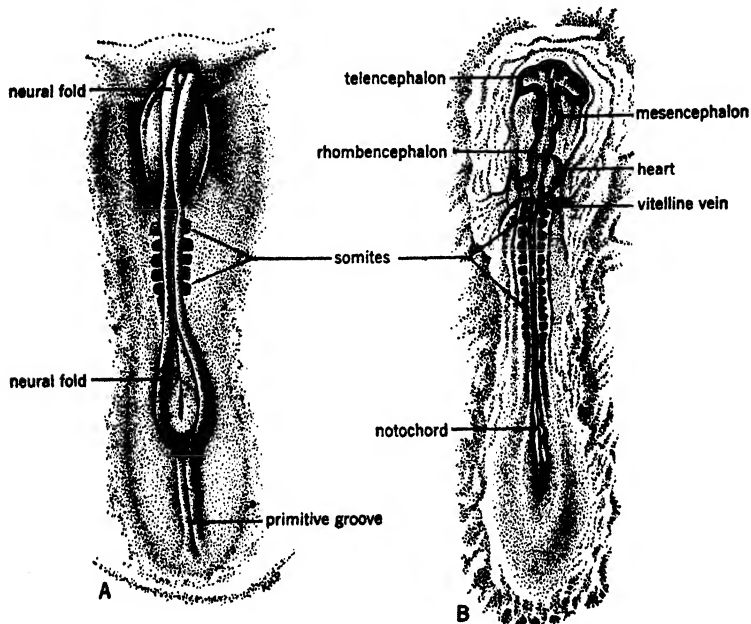


FIG. 63. A, 24-hour chick embryo. After Kerr. B, 33-hour chick embryo. After Shumway.

becomes the lining of the nervous system. The anterior part of the nerve tube now sends out outgrowths for the eyes and for the supra-segmental structures that appear on the dorsal side of the brain. The brain tissue differentiates into nerve cells of various types, and fibers for connections are formed and distributed. The cranial nerves grow out to innervate their structures, and, from the cord, neural crests appear that form the dorsal roots of the spinal nerves and the autonomic system. The peripheral system is an outgrowth from the central structure, the fibers extending out and elongating until they reach the definitive tissue that they are to innervate. From the motor region of the spinal cord, fibers are sent out that extend to the muscles, viscera, and other parts of the body (Fig. 63 A, B).

Eye

The eye is a rather complicated structure, since several sources supply the material used in its formation. From the forebrain, an out-pouching shows at an early stage, which finally pushes out towards the skin, enlarges, and becomes a double-walled cup. A groove known as a choroid fissure extends along the under side of the stalk from the cup to the brain. The outer wall of the cup forms the pigmented layer, while the inner becomes the retina. From the ectodermal layer of the side of the head, which is in close proximity to the optic cup, an invagination occurs, forming an ectodermal body, the lens of the eye. The eye becomes surrounded with mesoderm, which supplies the material to form the outer covering of the eyeball, muscles, and other accessory parts. The sensory cells of the retina are connected, through the optic stalk, with the brain, thus forming the optic tract (Fig. 63).

Ear

The ear is related to the lateral-line organs, and is formed by the invagination of the ectodermal auditory placode. The receiving cells are also ectodermal and derived from cells on the side of the head. The innervation and development both seem to point to a phylogenetic relationship with the lateral line. Starting as a pit, the vesicle differentiates into an utricular, vestibular, and saccular portion. The vestibular portion develops three ridges which pinch off and form the three semicircular canals. The attachment of the auditory pit to the ectoderm is marked by the endolymphatic duct in the shark. In higher fishes, the pit closes and the endolymphatic duct forms a connection with the meningeal spaces of the brain. The receptive cells of the ear are located in the ampullae of the three semicircular ducts and in the sensory patches of the sacculus and lagena. In tetrapods, a middle ear is added to the hearing apparatus, derived from the spiracular pouch, and other accessories are added, until the mammalian type is reached.

Nose

The formation of the nose is similar at first to that of the ear, since a sensory pit sinks down deep to form the olfactory cup. Except in cyclostomes, the olfactory pits are paired, and in close connection with the mouth. The nose undergoes several major modifications in changing from a water- to an air-testing device.

Taste

Taste buds, which are external receptors, are drawn into the mouth along with the ectoderm that lines this cavity, and may occur in the

mouth or pharynx. They may occur also on the outside of the body, as in some fishes, where they may be found on the head and sides of the body.

Skeleton

The skeleton is able to start its growth after the differentiation of the mesoderm, and, as this material insinuates itself between the other layers, the differentiation of the skeleton begins. The mesodermal cells are arranged in a layer around the body. The corium, immediately under the epidermis, is a source of skeleton building which makes up parts of scales, teeth, bony armor of primitive fishes, bony plates, the dermal plates of the skull, cleithrum, clavicle(?), episternum, gastralria, and other specialized parts.

Endoskeleton

In vertebrates, the nervous system is surrounded by a mesodermal layer, with horizontal and vertical septa, as well as material between the walls of the myotomes, and it is in this that the source of the skeletal material lies. The endoskeleton develops first by forming cartilage, which in turn changes to bone by a regular series of events through which the cells secreting the lime salts finally appear and dominate the growth.

Notochord

The notochord is a characteristic development of all chordates and is unquestionably the most primitive part of the skeleton. It has no predecessor in the invertebrates, and appears as a distinctive chordate feature. In *Amphioxus* (Fig. 61) it buds off from the dorsal side of the wall of the digestive tube, but in other forms it appears to take its origin from the primitive streak.

Muscular System

The muscular system forms simultaneously along with the skeletal system, and with few exceptions (ciliary muscle of the eye, and muscles of sudoriparous glands which are from ectoderm) it is from mesoderm. This includes the striated, smooth, and cardiac muscle. The mesoderm, arranged in sheets, along the sides of the embryo, becomes organized rapidly into mesodermal somites (Fig. 63), and these in turn become hollow and in cross-section show two walls, an outer and an inner. In a dorsal view of a developing embryo, these blocks show very distinctly at an early stage. The spaces between these blocks are invaded by mesenchyme cells so that a series of septa and cross septa

are built up. The cells of the embryonic muscle masses elongate, develop contractile threads, and soon assume the appearance of muscle cells. The myotomes extend ventrally and dorsally to the midline, forming the much-modified musculature of the head, gills, and neck, as well as the muscles of the body wall. The muscles of the limbs are formed by the downward extension of the myotomes into the limb buds, after the growth of the limbs. Besides the general body musculature, the involuntary system develops in the skin, around the viscera, blood vessels, and heart. This arises from the mesenchyme cells that have such a universal distribution throughout the body.

Digestive System

The digestive system (Figs. 60, 61) becomes tube-like and at either end has a short lining of ectoderm that has involuted at these two points, forming the stomodaeum or mouth cavity and the proctodaeum or anal cavity. The entire digestive tube, with these two exceptions, is lined with endoderm. There is an immense amount of activity in the digestive tract, and numerous outpouchings are produced to form the appendages of this system. The head region has teeth brought in by the infolding of the ectoderm where the scales become modified, changing their character and function. An evagination from the roof of the mouth, Rathke's pocket, becomes associated with an outpouching from the brain, forming the anterior lobe of the pituitary body or hypophysis. The pharyngeal region is intensely active also with a series of pouches, some of which are represented by the gill pouches and their derivatives. A similar series of pouches appears in vertebrates above the fishes, but they become much modified and have various functions. A series of glands associated with these pouches play a prominent part in both young and adult animals. In fishes, the pouches break through the body wall and develop gill arches; in most tetrapods above the amphibians the pouches do not break through, but leave a number of structures and glands as evidence of their former presence. The Eustachian tube of the tetrapod represents the remains of the first gill pouch, while the parathyroid, palatine tonsils, thymus, and epithelial bodies are proliferated from other pouches. The first outpouching posterior to the pharynx is the airsac of fishes, corresponding to the lung of the tetrapods. Posterior to the lungs, which starts as a median diverticulum, a single diverticulum forms the liver, and two or more form the pancreas. Other diverticula are present, such as the pyloric caeca of fishes and the caeca of reptiles, birds, and mammals; and there may be still other small outpouchings in the region of the rectum, such as the rectal glands of sharks or the bursa Fabricii of birds.

Circulatory Organs

Since metabolism must be carried on from the first cell divisions, the circulatory system is organized early in the development of the embryo, so that the activities may be carried on under optimum conditions. The disc of the vertebrate embryo, resting on the yolk, must tap this food supply, and a series of blood vessels form outside the disc, on the surface of the yolk. These form a capillary net that connects with the embryo through the paired vitelline veins and starts embryonic circulation. These paired veins, joined proximally, extend forward beneath the gut, ultimately swing to the dorsal side of the gut, and become the dorsal aortae. Later they fuse at the posterior end, forming the aortic arches (Fig. 63). The heart, at first a straight tube, assumes an S shape in fishes, the sinus venosus and the atrium being dorsal to the ventricle. In the higher vertebrates, a four-chambered heart is attained by septa which divide first the atrium and then the ventricle, thus changing a straight tube into a four-chambered heart (Figs. 63, 225).

Veins

The venous system develops at the same time as the arterial, to provide for the return of the blood, and this part of the system is much more complicated than the arterial. The primary parts are the two anterior and posterior cardinals. These must meet at the level of the heart where they form the ducts of Cuvier, which lead the blood into the sinus venosus and the atrium. This cardinal system is extended until it reaches all the organs. Veins conduct the blood from the posterior region of the body to the kidneys, where the vessels break up into capillaries and are conducted around the kidney tubules, while the intestinal blood is led to the liver, also breaking up into capillaries before being returned to the hepatic veins and the sinus venosus. The material forming the blood vessels, as well as the blood corpuscles, was termed angioblasts by His, and there is still some disagreement among embryologists as to the origin, but the greater majority consider the mesoderm as the germ layer that is the source of this material. In the forming blood vessels, cells called mesamoeboids appear, containing little haemoglobin, but as they develop into mature erythrocytes the haemoglobin appears.

Leucocytes may originate from this same mesamoeboid material. In mammals, the blood platelets are formed from parts of the protoplasmic processes of the giant cells developed in the spleen and bone marrow.

Urogenital System

The development of the urogenital system is usually taken back to the invertebrates, where the nephridia are paired in each segment, form-

ing an opening from the body cavity to the outside of the body. In vertebrates, this is much modified, and there is usually a connection between the urinary system and the reproductive organs. Developing from the mesomere of the mesoderm, the pronephros is the most primitive excretory organ, consisting of a small number of pairs (1-12) of tubules, a pronephric duct, and very primitive glomeruli. The vertebrates have segmental tubules and but a single pair of openings to the outside, through the pronephric duct, which collects the products of the tubules. The mesonephros is a continuation of the material from which the pronephros develops, and the tubules grow out posteriorly to the primitive pronephros, but many more tubules are present in each somite, since they may number several hundred. These two structures are closely related in structure and in origin, but, mechanically, the mesonephros is a decided improvement in a number of particulars. It uses the mesonephric duct, a derivative of the pronephric duct, as an outlet. The great improvement comes in the glomerulus with its capsule and its better blood supply. The metanephric kidney of reptiles, birds, and mammals, though closely related to the preceding structures, is quite different in that it is still more posterior in position, more compact, and has many more renal units. The nephrostomes or openings into the coelom are closed, and a new duct, the ureter, now carries the waste to the bladder. The metanephros is formed from two sources, as is also the mesonephros. A diverticulum extends dorsally from the base of the mesonephric duct until it meets the mesodermal ridge, projecting from the dorsal wall of the body cavity. This diverticulum and this nephrogenic cord form the kidney, with the ureter as the new duct. The new kidney has numerous renal units that unite and open into the pelvis or hollow of the kidney. With the loss of the nephrostomes, all connection with the coelomic cavity is lost. The long sinuous tubules have a rich vascular network, so that much activity takes place in this part of the renal unit.

Urinary Bladder

The urinary bladder is a variable structure in the lower vertebrates that may be present or absent in the fishes. The fish type is formed by the fusion of the lower ends of the Wolffian ducts and a part of the cloaca, thus forming a urogenital sinus. The Dipnoi have a dorsal diverticulum from the cloaca that is entirely different. The allantoic bladder which arises from the ventral wall of the cloaca is fairly stable and present in most forms. The base of the allantois is thus connected with the urinary sac, whereas the rest grows out to perform its respiratory and excretory functions. At birth, the allantois is cut off at the body wall, and the solid ligament connecting the bladder and the body

wall is the only trace remaining. The ureters retain their connection with the bladder as it grows, and the mesonephric ducts also retain a connection to the lower part of the bladder, which becomes the urethra or outlet.

Reproductive Organs

The testes and ovaries develop from the genital ridge, along the dorsal region of the coelom. The origin for both sexes is similar, but as they develop, they diverge widely. Growing out from the genital ridge, each retains a mesentery, the mesorchium of the male and the mesovarium of the female. The primordial male sex cells sink into the developing gonad but form seminiferous tubules that always enclose the spermatozoa; the primitive ova, in contrast, are imbedded in the ovary and must break through the wall to escape. The ducts through which the products of the gonads escape from the body are probably related. The males of all higher vertebrates use the Wolffian ducts to carry the sperm, and the females use the Müllerian ducts to carry the eggs. In the elasmobranchs these ducts form by a splitting of the original pronephric duct.

In reptiles, birds, and mammals reproduction is strictly terrestrial, and the eggs are fertilized internally. The genitalia are modified, and a male copulatory or intromittent organ is developed for depositing the sperm in the oviduct of the female. In the early embryonic stages of the mammals, the external genitalia of both sexes are quite similar, those of the female remaining quite simple whereas those of the male develop a penis, or intromittent organ, from the same structure that remains the clitoris of the female.

Fetal Membranes

The eggs of the fishes and amphibians, developed in water, have a yolk-sac, but this is the single feature of these lower vertebrates that approaches the fetal membranes present in eggs that are laid on land, or in eggs that are carried by the mother until born or hatched. Land life had a very decided effect on the egg and its development, and reptiles, birds, and mammals have three new membranes, the chorion, allantois, and amnion, which are to become the distinctive features of these classes.

Yolk Sac

The food of the embryo, the yolk, is enclosed in the body wall, by the development of the embryo. In fishes, a definite yolk-sac is surrounded by the intestinal wall, so that it becomes an integral part of the embryo.

itself. This material is gradually used up, and finally the yolk-sac is absorbed. Many fishes, after hatching, have a large yolk-sac still present, which is used as a food supply until its possibilities are exhausted. The large blood supply for the yolk-sac is necessary for the transportation of materials to and from the embryo.

Chorion

The chorion is formed by the outward growth of the body wall, which extends over the embryo in the head and tail regions, and finally fuses. The inner layer of this fold forms the amnion and the outer layer the chorion (serosa or false amnion). In birds and reptiles the chorion forms a protective envelope, but in mammals, it develops into a much more important structure and is directly concerned in the attachment of the embryo to the uterine wall (Fig. 56).

Amnion

The same fold that forms the chorion also forms the amnion, which is developed from the inner layer of this envelope, covers the embryo, and encloses it in a liquid-filled sac. This amniotic liquor is similar to sea-water in some respects, and replaces the ocean environment of eggs formerly laid in sea-water. The function of the amnion is protective, and the embryo in its liquid-filled cavity is insulated against minor shocks and disturbances that might injure the growing animal (Figs. 56, 57).

Allantois

A second outgrowth from the ventral part of the hindgut is a sac, which pushes out and enlarges until it may cover the whole embryo in reptiles and birds. In mammals, it contributes with chorion to the formation of the placenta or the structure that makes the connection between the growing animal and the mother. The allantois of reptiles and birds serves as a collecting organ for wastes, as a distributing organ for food materials, and as a very important organ of respiration. Its surface is covered with blood vessels so that functionally it is very useful to the embryo. In some ovoviviparous reptiles, the allantois may function as a connection between the embryo and mother, and the yolk-sac often serves in a similar way (Figs. 56, 57).

Placenta

Since viviparous forms appear in vertebrates, from fishes to mammals, it has been necessary for the embryos thus developed in the mother's body to have some means of disposing of wastes and of getting additional nourishment. The problem has been solved in a number of

ways, and the yolk-sac, hair-like growths on gills, hair-like growths from the uterine wall, have been the means of supplying this nourishment. Ovoviviparous reptiles may utilize the food supplied, but some other means of removing the waste and supplying food is desirable. The monotremes still retain reptilian and avian features in development, with the same use of membranes, since their eggs are enclosed in a shell and laid as in birds and reptiles. The marsupials are a stage in advance of the monotremes, but the young are born when very immature, and receive their nourishment through the mammary glands, to which they grow fast. Their fetal membranes are like those of the placentals, but the allantois, with few exceptions, does not make a contact with the uterine wall. The allantois of placental mammals always makes a contact with the uterine wall, and in these, the placenta reaches its highest development (Fig. 56).

P A R T T W O

**Comparative Anatomy of the
Vertebrates**

INTRODUCTION TO PART TWO

The Principles of Comparative Anatomy of the Vertebrates

Anatomy deals with the study of the structure of animals and in a strict sense includes the study of the microscopic structure of tissues and cells although these are usually separated under the studies of histology and cytology, the studies of organs and systems being left to the ordinary field of anatomy. Organs are composed of tissues which in turn are composed of cells. An organ such as the heart or the stomach contains many kinds of tissues that are derived from several different germ layers but are organized as a unit to perform a definite set of functions. Systems are groups of organs definitely organized to carry on one or more related groups of functions. In anatomy, the emphasis of study is directed to the gross structure and location of organs and systems and is more or less a study of the "geography" of the body.

Comparative anatomy is a more dynamic approach to the study of anatomy than the mere learning of the location and structure of organs and systems. Homologous structures in different animals are compared with each other to determine how these structures have originated and have become modified. Comparative anatomy seeks to show the phylogenetic origin of the various structures in different groups of animals by comparison of the form, location, and development of these structures. It seeks to explain why animals are constructed as they are and constitutes important evidence for the evolution of animal life.

The comparative method is based on a critical comparison of structures that are truly homologous rather than analogous. Homology deals with those structures that are alike in origin and fundamental structure. Analogy deals with structures that are alike in function and sometimes superficially alike in form but different in origin.

Homologous structures have the same origin but may be unlike in general form and function, as the classical example of the wing of the bird, the wing of the bat, and the arm of man. In a certain sense the

arm of man and the pectoral fin of the fish are partly homologous. Although additional development has added much to the basic structure of the human arm, the fundamental origin from the shoulder girdle is the same. Homologous structures are related and show a common evolutionary origin. Most structures are modifications of preceding structures and hence are homologous to those structures.

Analogous structures are those that are superficially alike in structure and have the same function but differ in origin and in basic structure. A good example is the caudal fin appearing in widely separated groups such as fishes, ichthyosaurs, and whales. Although this fin has the same function and looks fin-like, it originated as a different structure in each group, and careful examination will reveal a different basic structure. Analogous structures are not related by descent and hence show no common evolutionary relationship. When analogous structures of widely separated groups are similar in form they are said to exhibit "convergence" or "parallelism."

Analogous structures that arise for the same function and are associated with a similar environment, such as the development of fins in widely separated groups, are sometimes called adaptations. This term is often loosely used. Animals do not develop such structures to enable them to live in a certain place, but they live in that place because they happen to have developed suitable structures. "The survival of the fittest" has played a great role in the development and evolution of animal structures.

All vertebrates are built on the same basic scheme, and each system has its original fundamental plan. Most of these plans, but not all, were established very early, and the groups of vertebrates differ only because, as they develop, they modify or change the basic plan to reach their adult form. A few systems, such as the pulmonary system and the walking legs, came into existence with a new mode of life. But even these apparent innovations are based on pre-existing fish structures. Rarely is anything new added; sometimes innovations are made by modifications of old structures or more often by development of a part of the basic plan which has remained undeveloped (rudimentary) in preceding forms. These processes of change often leave structures without apparent function that tend to atrophy and disappear. These structures are known as vestigial structures. A common example is the human appendix.

Changes in vertebrate structures originate actually in the germ cell and not in the structure. The factors causing these changes are usually mutations; they operate by modifying the embryological development of structures. Modifications generally take place in the later stages of development. Hence, modified structures usually

pass through an early series of stages in which they follow the corresponding stages of preceding forms and change into their modified form in the later stages. Thus these factors have caused the wing of a bird to evolve from a reptilian fore leg with four or five toes. In the embryological development of the bird's wing, the structure passes through a stage in which four toes are easily recognized. Later one toe disappears, another becomes an atrophied stub, and the other two partly unite to form the distal part of the wing.

The history of individual structures, as shown in the attempt to work out the racial history or phylogeny of vertebrate structures, shows many gaps which paleontology does not cover. The racial history involves the establishment of a series of ancestral forms. It is difficult to determine the structure of ancestral forms as very few fossils are known which can be called ancestral. The comparative anatomist seeks to find living forms today that resemble the hypothetical ancestors and will bridge these gaps. The anatomist tries to determine the structure of the hypothetical ancestors by the study of the ontogeny or the developmental history of the individual, and, therefore, the embryological development of structures is important in comparative anatomy. In a general way the recapitulation theory, "Animals in their individual development (ontogeny) repeat the stages of the development (phylogeny) of the race," may offer clues to verify the relationship of structures and to establish hypothetical ancestral types. However, one must be alert to distinguish characters which are true repetitions of past history from those, such as fetal membranes, that have developed as embryological changes.

Ontogeny is not always reliable, as embryology shows that, ontogenetically, the skull of the higher vertebrates originates in cartilage whereas paleontology shows that, phylogenetically, the skull originates with much bone and later appears in cartilage. Ontogeny deals with embryonic structures, and these cannot be considered as adult. The stages revealed in ontogeny apply actually to past stages of embryological development. The gill arches that appear in the mammalian embryo are not vestiges of fish gills but are descendants of the gill arches appearing in fish embryos.

Some vertebrates even within the same group are highly specialized, whereas others are relatively generalized in structure. Ordinarily highly specialized forms offer fewer potentialities for future development. Paleontology shows that most ancient specialized groups have become extinct leaving no descendants but that present living forms have originated from more generalized ancestors. Generalized forms living today seem to be closer to the stem types and are of greatest importance to the study of comparative anatomy.

CHAPTER SIX

Integumental System

The integument has several important functions: the formation of a pliable covering for the body, resistant to the entrance of foreign materials; the regulation of body temperature; the prevention of the evaporation of the body fluids; the excretion of waste through the sweat glands; the development of sense organs; and the formation of special coverings and appendages. The prevention of evaporation is not important in animals living in water, but it becomes vital in land animals, which require a thicker skin with an exterior layer of cornified cells.

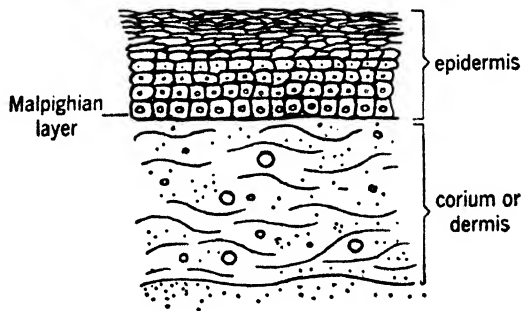


FIG. 64. Diagram showing structure of vertebrate skin.

The vertebrate skin consists of two layers: the outer layer, or epidermis, of ectodermal origin; and the inner layer, or corium derived from mesoderm (Fig. 64). The epidermis is a stratified epithelium and is usually thin. The epidermis may be divided into two main regions: an outer region of many layers of dead cells, which are usually flattened in land forms; and an inner basal region of a single layer of living cuboidal or columnar cells, called the Malpighian layer, or stratum germinativum, which is in contact with the nourishing materials of the corium. Blisters are formed by the separation of the outer region from the Malpighian layer. The Malpighian layer is continuously proliferating cells which are pushed outward to become horny and flattened. Thus new layers of dead cells are formed to replace those worn off on the outer surface.

Aquatic vertebrates have a thin epidermis which contains numerous mucous glands. The land vertebrates have a thicker epidermis. A number of structures, such as epidermal scales, feathers, hair, horns, nails, claws, and the enamel of the teeth, are all derived from the epidermis. The epidermis may contain poison glands.

The corium (Fig. 64), or dermis, is quite different from the epidermis, having a number of structures that are distinctive. This layer is usually thicker, and in its early embryological history it is derived from the outer wall of the epimere. The corium forms the leather of commerce. The main material of the corium consists of fibrous, connective, and elastic tissues, which give it strength. The corium is supplied with a rich series of blood vessels, with a network of capillaries and lymphatics extending over the whole surface of the body. Smooth muscles for the movement of the skin and its appendages are present. The sensory system consists of numerous types of sense cells, which are strictly specific in function, and some bare nerve endings in the form of a network. These sense cells may be quite close to the surface because of the folding of the epidermis. Sense cells are very plentiful on the finger tips and other restricted areas of the body. Most pigment cells are located in the corium, although a few may be found in the epidermis.

Bone is commonly developed in this layer, primarily in the formation of scales of the bony type such as those of the sturgeon or garpike. Secondly, this same type of bone formation is utilized in building part of the skeleton and the dermal bones come to be an important part of the skeletal system. All the dermal bones of the skull are considered to be modifications of scales or numbers of scales growing together in clusters to form bony elements. These dermal bones have Haversian canals and the structure of cartilage bone, so that in adults of the higher vertebrates there is no means of distinguishing materials of these two different origins. The jaws, or mandibles, originally made entirely of cartilage, have been surrounded with dermal or membrane bone, so that in the higher vertebrates Meckel's cartilage becomes but a vestige. Bones of dermal origin added to the shoulder girdle include the cleithra of fishes and amphibians and probably the clavicles. Parts of the sternum in certain of the reptiles have been added from the dermal layer, and the gastralia, or belly ribs, of the Crocodilia, *Sphenodon*, and *Archaeopteryx* are formed from this material. The teeth consist principally of dentine, a material from the corium, but the outer enamel layer is a contribution from the epidermis. All the special epidermal structures, such as scales, teeth, feathers, hair, claws, nails, and glands, dip down into the corium and retain a connection by which they obtain nourishment. Some of these structures are shed periodically; others retain a permanent connection with the corium.

Skin of the Different Classes of Vertebrates

The skin of *Amphioxus* consists of a thin dermis and but one layer of epidermal cells and in this it resembles the invertebrates. The placoderms, much lower than modern fishes in organization, had species with a covering of small denticles, as well as many species with well-organized systems of protecting plates.

Skin of Cyclostomes

Cyclostomes have a thin skin containing many unicellular mucous glands. Hagfishes have peculiar thread cells in the epidermis which throw out a fine thread. These threads entangle the copious mucous secretion and form a protective slimy coat over the skin. No scales or plates are present.

Skin of Fishes

The skin of fishes has a thin epidermis and a thicker corium or dermis, consisting of a loose layer and a compact layer. The epidermis is rich in mucous glands, which supply a protective coating, prevent the entrance of foreign materials and the growth of fungi, and make the skin smooth, reducing the friction in passing through the water. Poison- and light-producing organs may be present. In some fishes the scales develop from the corium alone; in others they develop from both layers of the skin. The scales, though subject to many variations, are of four general types: placoid, ganoid, cycloid, and ctenoid.

Placoid Scale. The placoid scale (Fig. 65) of the shark is one of the more primitive scales. It is important, since these scales on the rim of the jaw have given rise to the teeth found in all higher vertebrates. The placoid scale consists of a flat base, buried deep in the corium, from which a cusp projects to the outside of the skin. The scale is composed of dentine from the mesodermal corium and is tipped with a shiny substance which some believe to be enamel from the epidermis. There is some question, however, as to whether this is true enamel, although an enamel organ is present in the embryo. The substance is thought by some to be merely modified dentine. Each scale has a permanent cavity, large in the developing scale but reduced in the adult structure, filled with a pulp by which blood vessels, nerves, and other structures retain their connections. The shark tooth appears to be a placoid scale drawn into the mouth, with all the scale characteristics. In many sharks there is a perfect intergrading of the scales into teeth.

A very primitive bony fish scale is the type known as the cosmine scale which is found in the fossil crossopterygians and dipnoians. This

scale has an outer layer of dentine (cosmine) and an inner layer of lamellate bone with a middle layer of vascular bone.

Ganoid Scale. The ganoid scale is a collective name applied to a number of structures from quite different and unrelated fishes. These are heavy and quite complex in their structure, having a shiny coating

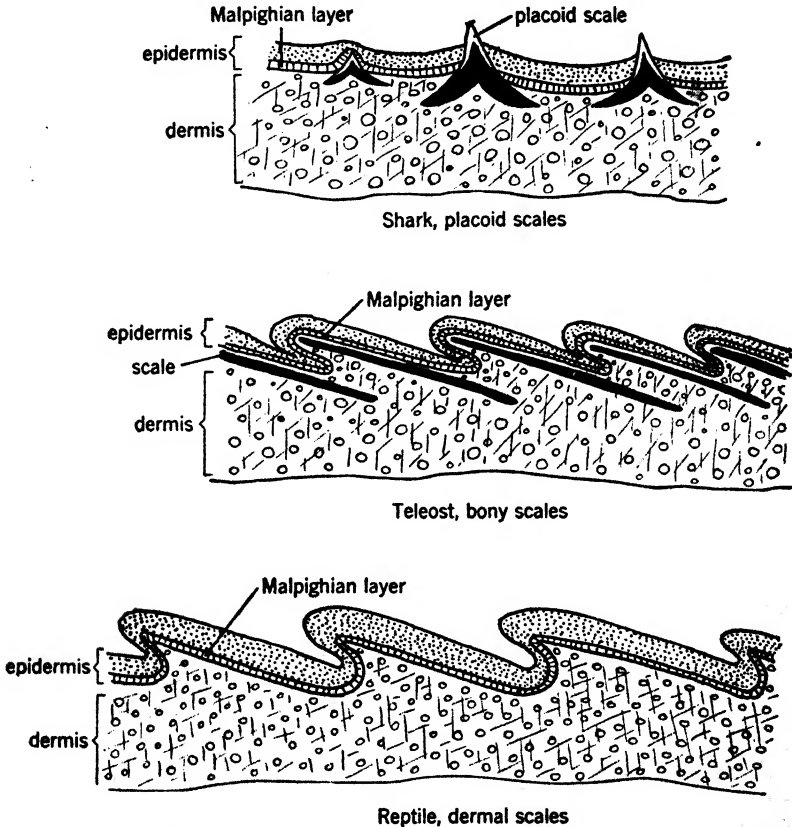


FIG. 65. Diagrams of vertebrate skin showing different kinds of scales.

of ganoin that is not epidermal in origin in spite of the resemblance to enamel. The scales of this type (Fig. 66 C) are generally rhombic in shape and do not overlap, but are joined by small peg-and-socket mechanisms which permit some movement. Once a very common covering of fishes, this type of scale is now restricted to a small number of species. The scutes, or plates, of the sturgeon represent a number of joined scales.

In some of the extinct Chondrostei and in the living *Polyodon* a modified scale known as the palaeoniscoid occurs. This scale

has an inner layer of lamellate bone and an outer layer of ganoin with a layer of cosmine in between. True ganoid scales lack the layer of cosmine.

Cycloid Scale. The cycloid scale is a thin circular bony plate derived from the corium and covered by a thin epidermis. It is found in *Amia* (Fig. 66), *Neoceratodus*, and many groups of teleost fishes.

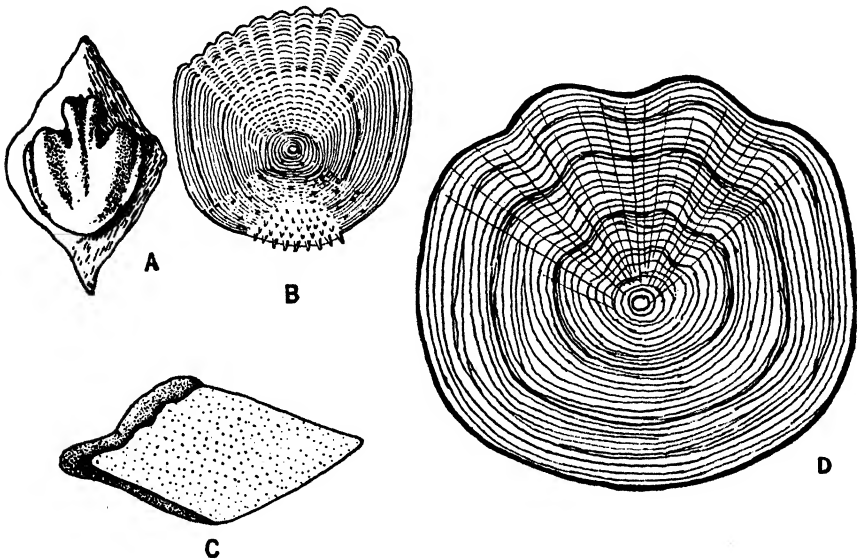


FIG. 66. Types of fish scales. A, placoid (shark); B, ctenoid (bluegill); C, ganoid (gar); D, cycloid (sucker).

Ctenoid Scale. The ctenoid scale is a circular scale differing from the cycloid scale in that the free edge is more or less serrated and the scale may be covered with tiny spines or prickles which may be soft, or harsh and rough. This type of scale occurs in many teleosts. Both ctenoid and cycloid scales are replaced when lost. They grow by the addition of bone to the margin-forming circuli. During the winter the growth is retarded and imperfect. Resumption of growth in the spring causes perfect circuli to be laid down over the imperfect winter circuli and produces a marked area, the annulus, which can be used to determine age.

Dermal Bone of the Fishes. The origin of the dermal bones may be seen in all stages in the lower fishes, where dermal plates are added to the chondrocranium and to other parts of the skeleton, and thus function in the building of bones. Such bones retain their characters as plating bones, with sculpturing and lateral-line canals, and those in the mouth cavity and the scales modified as teeth.

Dermal Fin Rays. Rays supporting fish fins are of dermal origin. Flexible unjointed rays of a fibrous material occur in the Chondrichthyes. Those of the Osteichthyes are generally branched, jointed bony structures and are thought to be derived from scales. The fusion of these gives rise to the stiff unjointed spines so common among the teleosts.

Skin of Amphibians

The skin of the amphibians (Fig. 67) is thin with large lymph spaces separating it from the muscle layer underneath. No scales are present in modern amphibians, except in the Gymnophiona which have them imbedded in the skin, although many of the fossil amphibians

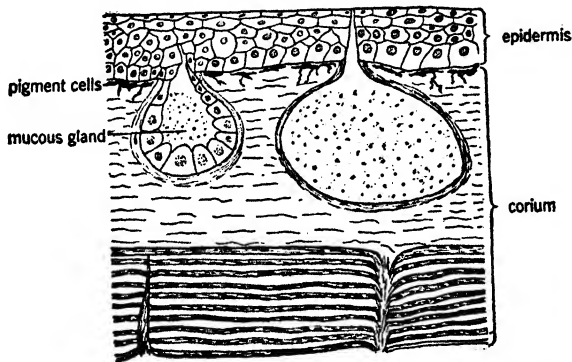


FIG. 67. Section of frog skin. After Schimkewitsch.

were well covered with scales. Chromatophores are usually present, and some members of this class have the ability to make decided changes in color. The skin of the amphibians is generally quite porous, since it serves a most important function as an accessory respiratory organ. A skin that will prevent evaporation is necessary for successful land life, and this is never quite achieved by the amphibians. The outer layer of skin, the epidermis, contains a large number of live cells, and only a relatively thin outer portion consists of dead keratinized cells which are shed periodically. Numerous mucous glands (Fig. 67) in the skin keep the skin moist, rendering possible the interchange of gases and counteracting the loss of moisture through evaporation. Toads have a slightly hardened epidermis and very large warty mucous glands. The mucus not only serves to keep the skin moist but may be protective, as it is acid and somewhat toxic in certain species. The great problem for amphibians is to prevent excessive evaporation of moisture through the skin and at the same time to use the skin as a secondary organ of respiration. The dermis of the

skin is richly supplied with capillaries, and a regular blood supply is maintained through the cutaneous artery. Thus an important respiratory aid is supplied since the lungs have insufficient area for the interchange of gases.

Claws are generally lacking among the amphibians.

Skin of Reptiles

Reptiles develop a dry skin that protects them from evaporation, thus enabling them to live a life entirely free from the water. In contrast to the thin epidermis of fishes and amphibians, reptiles have a thick epidermis composed of many layers of dead cells (Fig. 65). The skin of reptiles is usually rather impervious to water although in some desert forms, practically the entire body supply is from the dew that must be soaked in through the skin. Reptiles do not have the bony dermal scales characteristic of fishes; they usually are covered with either epidermal scales or dermal bony plates. The epidermal scale is formed by the folding of the epidermis on the dermis (Fig. 65); in the development of the bony plate a papilla is formed, similar to that in the development of the placoid scale of the shark. The epidermis grows continuously and the excess layers must be shed or rubbed off. Lizards and snakes shed the outer part of their epidermal covering periodically, often in one entire piece. Some of the extinct reptiles, particularly the water-living ichthyosaurs and the flying pterosaurs, had a smooth skin without scales. Others were covered with bony plates of dermal origin, such as are now found on the Crocodilia and on the head of *Heloderma* (Gila monster). Most modern turtles retain both the bony plates and the epidermal scales, and all of them have horny epidermal sheaths on the jaws. The soft-shelled turtles (*Trionychia*) and the leather-back sea-turtles (*Dermochelys*) have lost the epidermal scales and most of the bony plates, leaving a leathery covering—a return to water conditions.

Glands are rare in the skin of reptiles and are usually restricted to stink glands found around the anus of some snakes and turtles and to a few glands around the mouth. The males of some lizards have glands on the legs which, during the breeding season, secrete a substance that hardens forming spines used as holdfasts in breeding. In some lizards, such as the chameleon, the color changes rapidly owing to the automatic response of the chromatophores, or pigment cells, to surrounding conditions.

Reptiles may develop accessory skin structures such as spurs, spines, and horns. Claws are practically universal throughout the group. They apparently arise in the reptiles and are probably derived from modified dorsal and ventral scales at the end of each digit. The dorsal scale

forms the upper surface of the claw and is known as the unguis. The ventral scale forms the under surface of the claw and is known as the subunguis. The more rapid growth of the upper unguis causes the claw to be curved.

Skin of Birds

The skin is thin, consisting of two layers, the epidermis and the dermis. The skin is not glandular, the only large gland being the uropygial gland found at the root of the tail and used for giving an oily coat to the feathers.

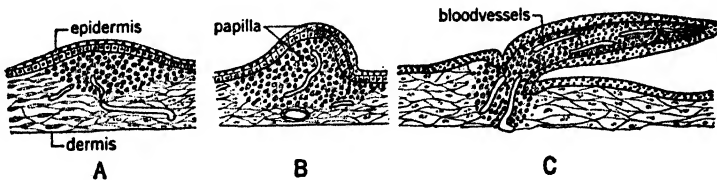


FIG. 68. Developing feather. A, early stage of papilla; B, papilla enlarged; C, early stage of feather.

The typical covering of birds is the feather, which is considered a modified scale. Feathers are not distributed uniformly over the entire body, but are confined to areas called pterylae, in contrast to the apteria, or areas without feathers. Feathers are shed at intervals, usually in the summer so that the plumage is complete at times of migration and during the cold seasons. The feather (Fig. 70) is admirably adapted to the needs of birds, since it is light, warm, and strong, and hence serves both as a flight structure and as an insulator. Feathers are divided into several types, each with its special uses: (1) pennae, the typical contour feathers; (2) remiges, or flight feathers; (3) plumulae, or down feathers; and (4) filoplumes, or hair feathers. Feathers of a fowl vary from the perfect specimen, in which all the typical parts are present, to the hair-like feather in which only the shaft is left. The perfect feather (Fig. 70), such as the flight feathers, consists of a shaft, with two parts, a base, or hollow quill, and the rachis, to which the vane is attached. The vane consists of a series of barbs, extending out from the rachis, which, in turn, have a series of small processes, the barbules. Barbicels, or hooklets, fasten the barbules and barbs together, so that a disarranged feather is easily repaired. The inferior umbilicus opens at the base of the quill, and the superior umbilicus at the base of the vane. The feathers covering the body are similar in structure to flight feathers. When the hooklets are absent the feathers are downy, as in the down of geese, ducks, and young birds generally. The presence of many of these plumulae

gives the birds a fluffy appearance, in contrast to the smooth-feathered adult. A third type, the hair feather or filoplume, consisting only of

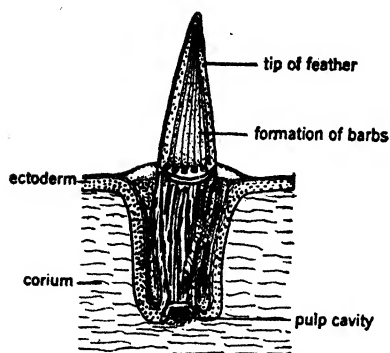


FIG. 69. Developing feather in follicle.

the shaft, is found around the eyes and under the other feathers. Coloring, so striking in birds, is due primarily to pigments in the feathers and secondarily to their prismatic surfaces which give rise to iridescence.

The development of the feather (Figs. 68, 69) is similar to that of the scale, the origin being a papilla formed from the dermis, with an epidermal covering. This sinks in slightly and comes to lie in a feather follicle, from which the growing feather protrudes. The completed feather is purely ectodermal. Although the feather is considered a modified scale, the process of its trans-

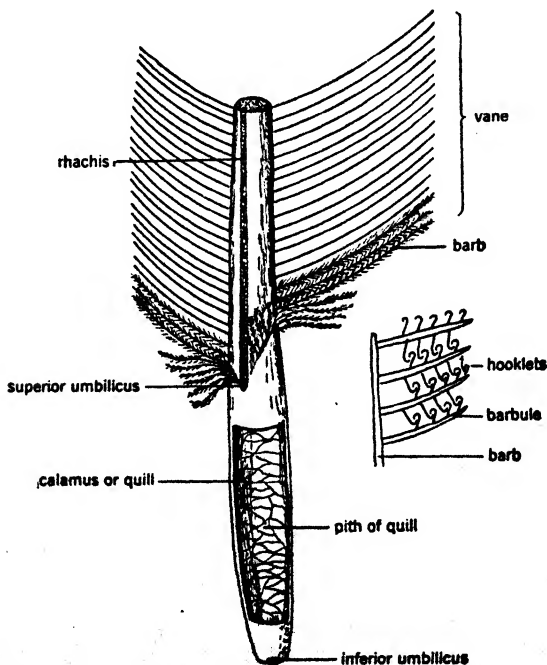


FIG. 70. Parts of a feather.

formation is entirely unknown and remains a problem. The first known bird, *Archaeopteryx*, had fully developed feathers. In modern

penguins the feathers of the wing revert to scale-like structures once more.

Birds have but few epidermal structures aside from the feathers. Epidermal growth forms the spurs on the legs of many birds. Vestigial claws may occur on the wings of a few birds such as the hoactzin. Birds retain reptilian claws on the toes of their hind legs. The bill has a horny epidermal sheath, and the legs retain reptilian scales. It is probable that the horny sheath of the bill was not present in early forms, such as *Archaeopteryx*, which had teeth.

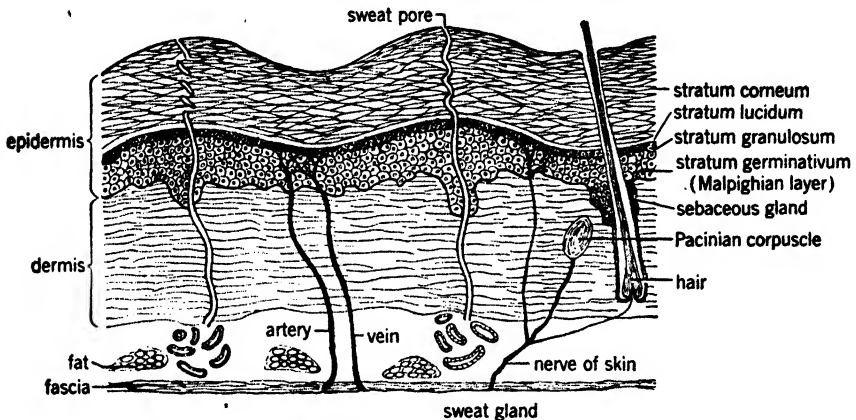


FIG. 71. Diagram of section of human skin.

Skin of Mammals

The skin of the mammals is of the typical land type with a cornified layer of dead cells forming the outer layer, or corneum (Fig. 71). Under this is the growing Malpighian layer, which is in contact with the corium. No living cells are exposed to the air except those around the orifices. The greatest specialization of the two layers is reached in the mammals, with their high differentiation and general adaptability. The most striking difference between the skin of mammals and that of all other vertebrates is the presence of sudoriparous, sebaceous, and mammary glands. In general the mammalian skin, with its higher development of the corium, is thicker than that of the lower forms. The covering is hairs, instead of scales or feathers.

All mammals possess hair although it is scanty on some, such as the Cetacea and the Sirenia. In general mammalian hair can be divided into two types on the basis of growth: most mammalian hair has definitive growth and reaches only a certain length, after which it falls out and is replaced; some hair has indefinite growth such as

the hair of an Angora goat and the long hair of the human head and beard.

The development of the individual hair parallels that of the feather and scale. It starts by a thickening of the epidermis which dips down into the corium, and from this pit a solid horny shaft is pushed outward by the rapid growth of these specialized epidermal cells, which get their nourishment from the corium. This connection remains, and when the hair is shed the break is well above this root, or matrix, so that regeneration follows easily. The hair itself becomes organized and divided into regions, a central medulla, a middle cortex, and an outer cuticle. Small muscles in the corium are able to change the position of the hairs, thus causing the gooseflesh evident when the human body is exposed to sudden cold. In humans before birth an embryonic coat of hair, the lanugo, is quite evident but is shed soon after birth. The

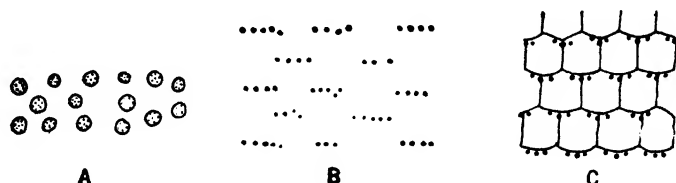


FIG. 72. Grouping of hairs in mammals. A, beaver; B, monkey; C, rodent. After Meijere.

hair pattern (Fig. 72) is quite regular and seems to suggest that the first hairs developed around scales, a condition still to be found in the armadillo.

There are many modifications of hair in the mammals, due to differences in both structure and shape, an extreme being reached in the porcupines with their special quills. Horns of the type found in the rhinoceros and antelope appear to be formed by bundles of hair massed together. The shape of the hair may be cylindrical or flattened and roughened on the outside. The soft wool of animals such as the sheep or beaver is hair with a tendency to curl, because of the flattened shape and rough exterior, which aids in felting. The eyes are usually protected by elongated hairs, the eyelashes; and whiskers, or vibrissae, which have a well-developed nerve supply at their bases, may grow around the mouth. The hair is arranged in stream lines pointing in different directions. In man there is usually a whorl in the occipital region; in other mammals there may be a number of these whorls in different regions of the body. The hair carries pigments, giving black, brown, or reddish colors. Melanistic and albinistic mammals are not uncommon.

Scales appear commonly in the mammals and seem to be a part of their heritage from the reptiles. Embryos may show scales or spines that are not at all evident when they are born. The embryo of the bear has a complete development of spines in the skin which are entirely lost with further growth. Scales appear on the tails of many mammals, including the rats, mice, muskrats, and beaver, but they are not overlapping, and hairs are interspersed between them. The feet of kangaroos are strikingly scaled, even in the adult stage, and the palms and soles of other mammals, including man, show many evidences of a scale pattern. The most perfect mammalian scales are found in the pangolins; they are purely epidermal scales, often two inches in length, which overlap and have the typical reptilian arrangement. Bony plates are found principally in the edentates; the armadillo, a modern representative of this once large group, is completely covered with bony plates, with hairs arranged around the edges.

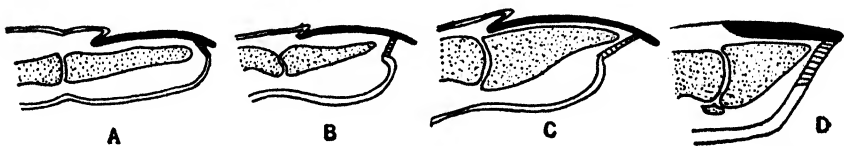


FIG. 73. Sections of claws and nails. A, nail; B, claw; C, claw; D, hoof. Redrawn from Boas.

The mammals have inherited the reptilian claws which may be modified into hoofs and nails, highly specialized in mammals (Fig. 73). The claws fit over the ends of the last bones of the digits and are modified cones in appearance. Without specialization, the claws (Fig. 73 C) protect the ends of the digits and may give some traction in walking. By broadening and strengthening, they are fitted for digging, as in the badger or the mole. Those used for climbing are thin and sharply pointed, and by their aid semiarboreal mammals are able to live in trees. The cats have developed sharp, curved claws that are very useful in holding and killing their prey. The hoof (Fig. 73 D), found principally in the "ungulates," is a modified claw with a broad subunguis, the unguis forming the contact with the ground. In the horse the hoof is developed from the claw of only one toe, with no other parts of the foot touching the ground. Other hoofed animals may use other parts of the foot, or may be provided with spongy pads (subunguis), such as are found in mountain sheep, where a hard hoof would not serve well for rock climbing. The nail (Fig. 73 A, B), perhaps the highest development, is found in the higher primates and in a few species of other orders. It is a flattened unguis that does not form a cap over the end of the digit, but merely forms a dorsal plate. The subunguis

is greatly reduced. The Cetacea have lost their claws and have the ends of the digits naked.

Horns are conical, epidermal caps that develop on solid cores arising from the frontal and parietal bones. The median horn of the rhinoceros appears to be formed from firmly appressed hairs on a bony core, and it is quite possible that other horns have the same organization. Horns grow continuously and are not shed except in the antelope (*Antilocapra americana*), which sheds a part of its horn and which also is the only mammal with a branched horn. If horns are lost, some regeneration takes place depending on the extent of the injury to the underlying corium and bony core. Generally but one pair is present, but some of the domestic breeds of sheep (Navajo sheep) have two well-developed pairs. Some of the early mammals (titanothere) had several pairs of horns. In modern mammals, horns and antlers are practically confined to the Artiodactyla.

Antlers are entirely different from horns, since they are formed from bone and are usually branched. They start their growth as small protuberances on the skull bones, usually the parietals, and remain covered by a layer of living epidermis until they have attained their full size and growth. This epidermal skin is called the velvet and is coated with hair. After growth is completed, the epidermal covering loses its vascular connections, dies, and is rubbed off, leaving the antlers composed of bone, which also dies and becomes highly polished. Some of the antlers of the deer group are enormous, those of the extinct Irish elk having a spread of thirteen feet. Antlers are shed annually by means of the formation of a constriction below the burr, so that they are easily dropped off in the winter or early spring, an immediate new growth starting for the next pair.

Glands. In contrast to the almost glandless skin of the reptiles and birds, that of the mammals is richly supplied with several types of glands. (Skin glands are lacking in whales and sea-cows.) Both the sweat (sudoriparous) glands and the oil (sebaceous) glands appear to have their origin in connection with the growth of the hair, and, whereas the oil glands usually retain this association, the sweat glands are generally spread over the skin. The oil glands are acinose in form (like a bunch of grapes) and have their outlets along the side of the hair. In the region of the eyes the Meibomian glands become separated from hair. ✓

The sudoriparous glands are tubular, opening through the epidermis by means of pores. They extend through this layer of the skin by a coiled tube, and the body of the gland itself is deeply imbedded in the corium, where it is in contact with the capillaries. Perspiration is a means of elimination of salts and other waste matters, besides being

an aid in the stabilization of temperature. The nature of the secretion varies, since in man it is watery and colorless, in the horse it is mucilaginous, and in the hippopotamus it has a distinct red color.

✓ Scent glands, which probably have a function connected with sex, are modified sebaceous glands, and hence are of the acinose type. These include the anal glands of the skunks and other Mustelidae, suborbital glands of the deer, preputial glands of the beaver and musk deer, temporal glands of the elephant, and numerous other glands found in other orders✓

Most striking of all are the mammary glands, by which the mammals are distinguished as a separate class of the highest vertebrates. These milk-producing glands are tubular, and this is one reason for assum-

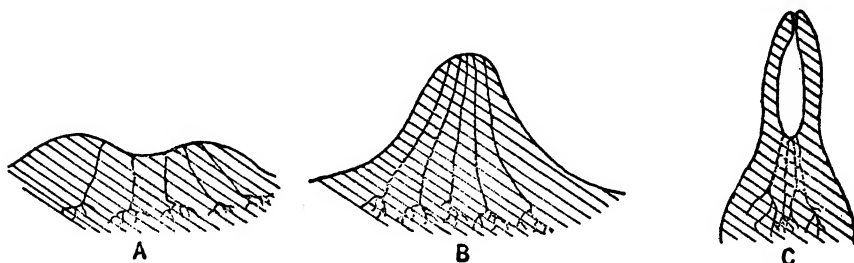


FIG. 74. Schema of developing nipples. A, primitive condition as in monotreme; B, nipple found in marsupials and some placentals; C, ungulate mammal.

ing that they originated from modified sweat glands. They probably became specialized in connection with certain brooding areas or ridges on the ventral sides of the females, similar to the ridges that develop in birds while incubating eggs. Originally the fluid from these glands poured out over the surface, as in the monotremes, with no nipples (Fig. 74). The system is more specialized in the marsupials, where nipples are present, and it reaches its highest development in the placental mammals, where the glands are closely associated with the bearing of the young and function during their infancy, drying up later when no longer needed. This milk-producing function is intimately associated with the longer period of infancy.✓

Teeth

The origin of teeth appears to have been from placoid scales, and a comparison of the development of both is quite convincing, since the processes are practically identical, each starting in the same way and carrying through to a mature structure in a similar manner (Fig. 75). The presence of teeth in the mouth can be explained by the fact that, in the developing embryo, the oral cavity comes to be lined by a layer of

ectoderm that is drawn in from the surface, carrying with it its tendency to develop epidermal appendages. In some of the elasmobranchs it is possible to trace a graduated series of scales into the mouth cavity, with no break in the continuity. Even in the higher vertebrates, such as the mammals, tooth formation follows the same general plan as in the development of the elasmobranch placoid scale and leaves no question as to their origin.

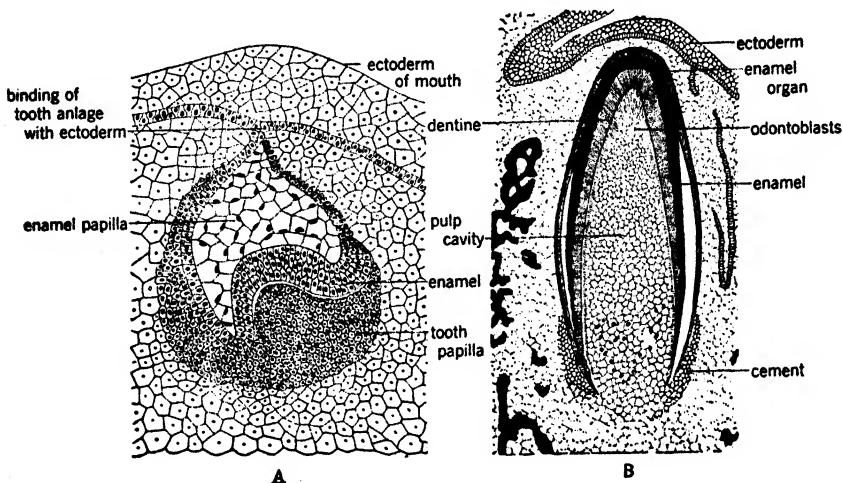


FIG. 75. Developing teeth of pig, slightly diagrammatic. A, developing molar showing the relation of the growing parts and the formation of the tooth; B, developing canine tooth.

Whereas the teeth of all the lower vertebrates are comparatively simple cone-like structures, the teeth of mammals become highly specialized, with additional cusps and often with very intricate patterns on the grinding surface.

The rasping spines of the cyclostomes are of purely epidermal origin, contain no dentine, and are not true teeth. The epidermal teeth that develop as temporary structures in young amphibians are lost later or replaced with real teeth. Epidermal plates, not comparable to teeth at all, appear in turtles and modern birds, where they serve to protect the jaws. The monotremes have real teeth in their developmental stages, but these are lost and replaced by epidermal plates in the adult forms (duckbill).

The attachment of teeth to the jaws is quite variable in the vertebrates. In fishes, amphibians, and some reptiles, the teeth are lost and replaced constantly (polyphyodont), but in a few reptiles and in mammals there is a more limited growth of new teeth, only one (mono-

phyodont) or two sets (diphyodont) being developed. Those of the sharks are fixed to the jaws by fascia and tough connective tissue. The manner of attachment to the jaws is called acrodont (Fig. 76 A) if the tooth is placed upon the crown of the jaw, pleurodont (Fig. 76 B) if it is ankylosed to the inside of the jaw, and thecodont (Fig. 76 C) if it is in a pit on the crown of the jaw. With the development of the higher types of teeth and relative permanence, roots are formed, and there is a specialization of the pulp cavity for nourishment.

Teeth of Fishes

Teeth may appear on almost any bone of the oral cavity of fishes. There is a striking development of teeth in the sharks (Fig. 77 A, B) most of them

having a general similarity in shape not found in any of the other fishes. Some have several cusps, and many have serrated edges, but all are very effective cutting instruments. The peculiar "pavement" teeth of some of the rays mark them as eaters of molluscs; other carnivorous fishes, such as the pike, garpike, pickerel, and bowfin, have long, sharp, needle-like teeth (Fig. 77 C, D, E). Crushing teeth are found in some of the teleosts. The wolffish (*Anarrichthys*) has a very

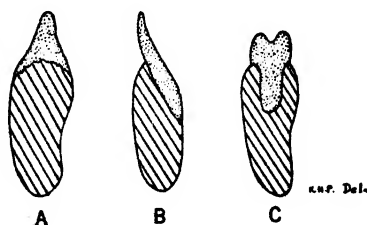


FIG. 76. Different types of tooth attachment. A, acrodont; B, pleurodont; C, thecodont.

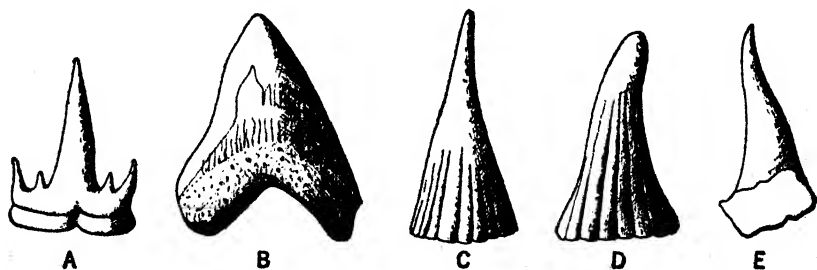


FIG. 77. Teeth of fishes. A, *Cladodus* (after Dean); B, *Carcharodon*, an Eocene shark; C, *Lepisosteus*; D, *Anarrichthys*; E, *Esox*.

efficient series of heavy crushing teeth (Fig. 92), well adapted for the use of this fish. Most fishes have teeth that are all alike, a condition known as isodont. The teeth are greatly reduced or absent in some of the teleosts, and their food requirements are such that teeth would be of no particular value. The spoonbill (*Polyodon*) and other fishes that live on plankton, obtained by straining water, are more or less toothless. The peculiar tooth-like

structures appearing on the pharyngeal bones of the carp and many other teleost fishes, though used as teeth and covered with an enamel-like layer, have a different origin and are not homologous to other teeth.

Teeth of Amphibians

The teeth of modern amphibians are always small, needle-like, and inconspicuous and are but little differentiated. The fossil amphibians had large teeth, often with a very complicated enamel pattern, as in the labyrinthodonts. The attachment is usually to the side of the jaw and hence pleurodont. The distribution of the teeth is more restricted than in the fishes, since they generally are found only on the premaxillae, maxillae, palato-ptyergoids, coronoid, dentary, and vomeropalatines, but not on other bones of the oral cavity.

Teeth of Reptiles

Reptiles are generally provided with teeth. The turtles are the exception in having no teeth and in being provided with horny plates comparable to those of the bird bill. The teeth may be divided into two groups, those suited for animal food and those specialized for herbivor-

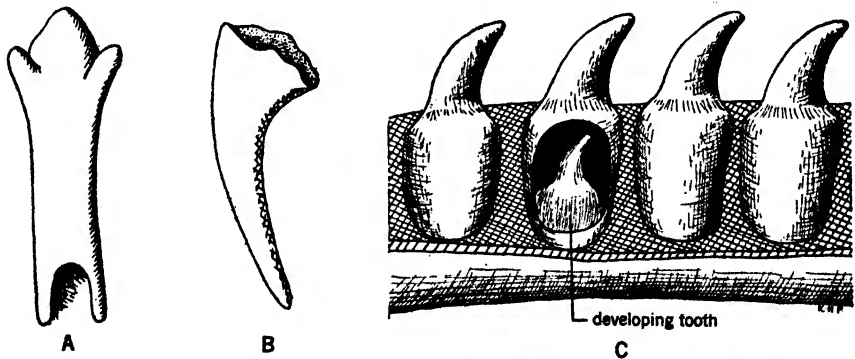


FIG. 78. Teeth of reptiles and birds. A, iguana; B, python; C (after Marsh), *Hesperornis regalis*, showing developing teeth.

ous diet. There is a constant loss and replacement of teeth (polyphyodont), with little of the permanency found in the mammals. The attachment may be acrodon as in *Sphenodon*, or pleurodont as in the iguana (Fig. 78 A), or thecodont as in the alligator. With the exception of the Therapsida, no order or group has any specialization of the teeth that would suggest the mammalian dentition. Reptilian teeth are generally all alike or isodont. Inasmuch as most reptiles swallow their food whole, the most efficient tooth for them is one that is long and sharp enough to assist in holding the prey, and this is the ty-

found in carnivorous forms. The extinct fish-eaters, such as the ichthyosaurs, had needle-like teeth, superficially resembling those of the fishes, such as the garpike, that get their food in a similar manner. The carnivorous dinosaurs (*Tyrannosaurus*) had teeth that were dagger-shaped, with sharp edges, so that they were of value in killing as well as in holding. The teeth of the snakes (Fig. 78 B) are very long and sharp but rather weak. The poison fangs are developed for the special purpose of introducing the venom into the wound and are not essentially killing teeth. A tube for the passage of the poison is formed by a secondary fold of the wall of the tooth (Fig. 79 A, B, C).

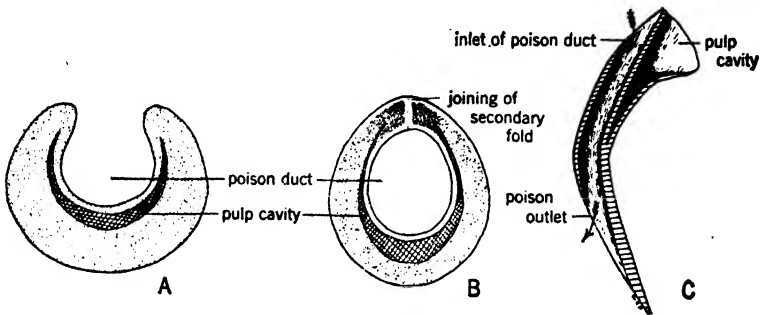


FIG. 79. Poison fangs. A, cross-section of grooved tooth of *Heloderma*; B, cross-section of fang of a rattlesnake; C, sagittal section of poison fang of rattlesnake.

The herbivorous reptiles have teeth with flattened crowns, which form a grinding surface. The teeth of *Trachodon* and other dinosaurs of this type were very efficient in handling masses of vegetable material. The most extreme crushing dentition is that found in the fossil *Placodus*, and the arrangement suggests that the animal lived around or in water and used the teeth for crushing molluscs and other shelled food. The cynodont reptiles had a dentition that was approaching the mammalian type since their teeth were divided into incisors, canines, premolars, and molars. Their molar teeth had the incipient cusps that suggest the future mammalian evolution.

Teeth of Birds

Only the earliest birds had teeth. In *Archaeopteryx* of the Jurassic period and in *Hesperornis*, *Ichthyornis*, and other birds of the Cretaceous period, the teeth were typically reptilian and were probably useful in food-getting. *Hesperornis*, a diver, living in the Cretaceous sea of Kansas, certainly could make good use of the sharp-pointed teeth (Fig. 78 C). Teeth do not appear in any birds of the Tertiary or Quaternary periods, although they can be demonstrated in the developing young of some modern forms. Ducks have an adaptation of the

horny covering of the jaws that forms a strainer, and in the fish-eating ducks the serrated edge of the mandible serves for holding the prey.

Teeth of Mammals

The mammalian dentition becomes highly specialized with a number of features not found in the reptiles. Instead of a constant replacement, the number of sets of teeth is limited. Usually the first or milk set is shed and is followed by a permanent set that must last throughout the life of the animal. This type of dentition is known as diphyodont. A few mammals such as the sirenians and some toothed whales are said to be monophyodont and have only one set of teeth. The differentiation of the teeth into various kinds (heterodont) initiated by the therapsid

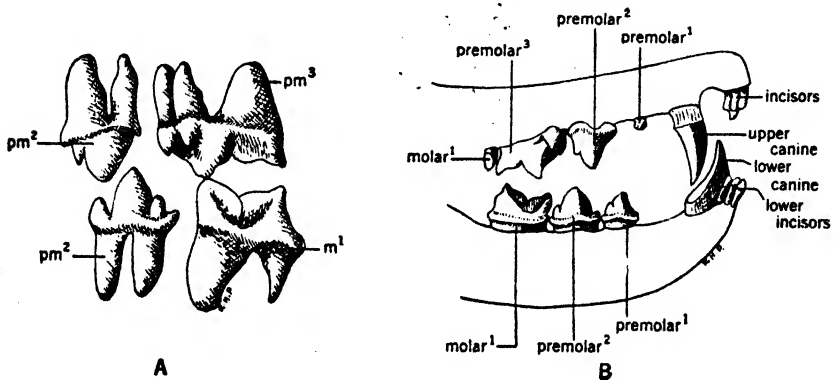


FIG. 80. Occlusion of teeth in cat. A, occlusion of the shearing teeth; B, occlusion of the entire dentition. After Jayne.

reptiles is continued, with standardization of the teeth into four kinds: incisors, canines, premolars, and molars (Figs. 80, 81). With few exceptions, the teeth are set in alveoli and held in the jaw by single or multiple roots. If the roots remain open, the growth of teeth may continue through the life of the animal; but if the roots close, so that only a small foramen remains for the nerve and blood vessels supplying the pulp cavity (Fig. 81 A, B), growth stops at a definite point. There is much diversification of the teeth themselves, with cusps of different types developed in connection with food specialization. The number also reaches a certain standardization with the following formula as fairly typical:

$$\frac{3-1-4-3}{3-1-4-3} = \frac{3 \text{ incisors}}{3 \text{ incisors}} + \frac{1 \text{ canine}}{1 \text{ canine}} + \frac{4 \text{ premolars}}{4 \text{ premolars}} + \frac{3 \text{ molars (in each half of the upper jaw)}}{3 \text{ molars (in each half of the lower jaw)}}$$

The division of the teeth into different types in the mammals has enabled them to specialize in ways not possible to the reptiles. The incisors (Fig. 80 *B*) are small in carnivorous animals, where they are used in a limited way, but in the herbivorous types they assume great importance, as in the rodents. The canines (Fig. 80 *B*) assume great importance in the carnivorous animals, serving for both killing and tearing; they are extremely large in many carnivores, but may be

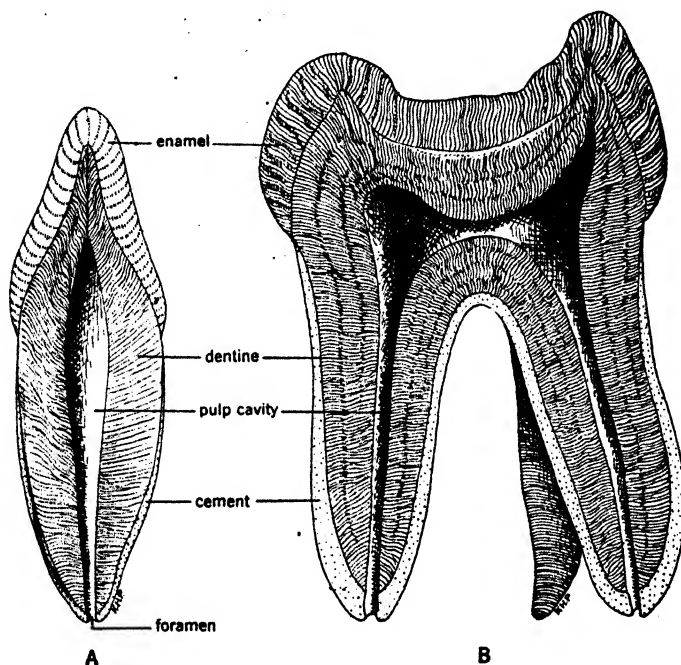


FIG. 81. Section of teeth to show structure. *A*, incisor; *B*, molar. After Weber.

altogether absent in herbivores. The premolars and molars (Figs. 80 *B*, 81 *B*) have much the same use in the herbivores, but in the carnivores there is a tendency to develop certain of these into shearing teeth for meat-cutting (Fig. 80 *A*, *B*). The toothed whales are isodont (homodont), showing no differentiation in the teeth.

From a study of the dentition of the older mammals, Cope and Osborn developed a theory that the primitive type of the mammalian tooth was tritubercular, that is, with the three cusps in a triangle. According to this theory, the single spike-like haplodont (Fig. 82 *A*) tooth is considered the original element from which the more complicated teeth have been derived. The protodont tooth (Fig. 82 *B*), as found in the lowest fossil mammals, has small projections developing along the

sides, but with rather an indefinite organization of the cusps. The triconodont tooth (Fig. 82 *C*) has three definite cusps, all in a line, the central cusp usually larger and longer than the others. The turning of the smaller, lateral cusps produces the tritubercular tooth (Fig. 82 *D*) in which the cusps form a triangle, with the position reversed in the lower jaw, so that there is close occlusion. The number of cusps may increase to four or five or more, and one primitive group has a multitubercular pattern (Fig. 82 *F*).

The theories of R  se, Bolk, and others arrive at the same tritubercular tooth pattern, but in a different way, since they consider that the process of cusp-building was through the combination of small,

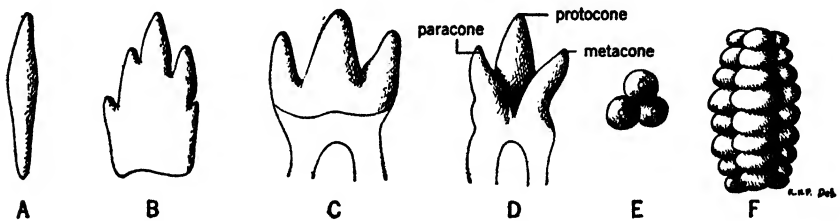


FIG. 82. Development of tooth cones. *A*, haplodont; *B*, protodont; *C*, triconodont; *D*, tritubercular; *E*, triangular arrangement of cones in tritubercular; *F*, multitubercular. After de Terra.

single-cusped teeth which would join together and thus form the tritubercular stage. The theory of R  se is called the concrescence theory and is based upon the formation of teeth combined from several single elements that appear in sharks, and from some considerations of conditions that occur in the development of the teeth of mammals themselves.

The discovery of a number of small Cretaceous mammals in Mongolia, and the restudy of the whole Mesozoic series of early mammals by G. G. Simpson, have shed much light on the evolution of the mammalian teeth, long a controversial subject among paleontologists. Although the main idea of the Cope-Osborn theory may be retained, certain details of the shifting of cusps in both the upper and lower molars must be restated, since some of their shifts of cusps and homologies of cusps have not been supported by paleontological evidence.

The evolution of the teeth has had a very significant bearing on the development of the mammals, since it has been so closely associated with their various specialized food habits. Throughout the whole series of animals below the mammals, there have been specializations, such as teeth with serrated cutting edges, sharp-pointed teeth, crushing pavement teeth, and sharp incisor-like teeth, all of

which appeared in the fishes. The amphibians show little variation in tooth form, but the reptiles have had quite a wide range with the sharp-pointed, crushing, herbivorous pattern of some dinosaurs, and even poison fangs, all of which gave them a much wider food range.

The Mesozoic mammals had the cusp system well established, and the typical triangular pattern appeared in several of these groups, such as the marsupials and the insectivores. These first molars have three cusps, forming a triangle, the apex of the triangle pointing inward in the upper series and outward in the lower teeth. The three primary cones of the upper molars are the protocone, paracone, and metacone; those of the lower jaw, the protoconid, paraconid, and metaconid. An additional hypocone and hypoconid form the four-cusped molar. Additional cusps may form four-, five-, or six-cusped teeth. These cusps are very useful in tracing the relationship of animals, since the tooth pattern is often quite specific. Starting with the Tertiary period there was a very active evolution in the teeth and the development of all the modern patterns. Originally pointed, these cusps may become rounded, flattened, and joined with ridges to form sharp shears as in the carnivores, or joined to make areas called lophs as in the horse.

The height of the crown varies from the low-crowned (brachydont) type as found in the cow, to the high-crowned (hypsodont) type as found in the horse. The tooth surface becomes highly specialized in the mammals, the carnivores developing a dentition (secodont) in which the teeth are specialized for meat-eating. This carnivorous dentition is found in a number of the orders, including the moles and shrews (Insectivora), some marsupials (polyprotodonts), and the bats (Chiroptera). The carnivorous dentition varies from the most specialized type as found in the cats, to the modified, rounded, crushing cusps found in bears. The herbivorous animals including the hoofed groups such as the artiodactyls and perissodactyls have a dentition (selenodont) (Fig. 83 A) in which the enamel is folded with cement introduced between the folds, so that, with the unequal wear, hard enamel ridges remain, thus forming sharp grinding surfaces (Fig. 83 E). This is modified in the horse (Fig. 83 B) by the formation of cross ridges and crests (lophodont) (Fig. 83 C), and, although the dentition is useful in grinding, it is not able to crush and cut vegetable fibers as does the selenodont type. The teeth of pigs are modified by the formation of rounded cusps (bunodont) which supply them with a dentition suitable for their omnivorous habits. Sometimes the types are mixed, as in the ancient titanotheres, in which the selenodont was combined with the bunodont, half of the tooth with cutting edges and the other half with rounded cusps. Since the type of dentition is closely correlated with

the food habits, it is quite possible to determine these from a study of the dentition alone.

Occlusion of the Teeth

By far the most important single character of any dentition is the meshing of the upper and the lower teeth when in use. If dentitions

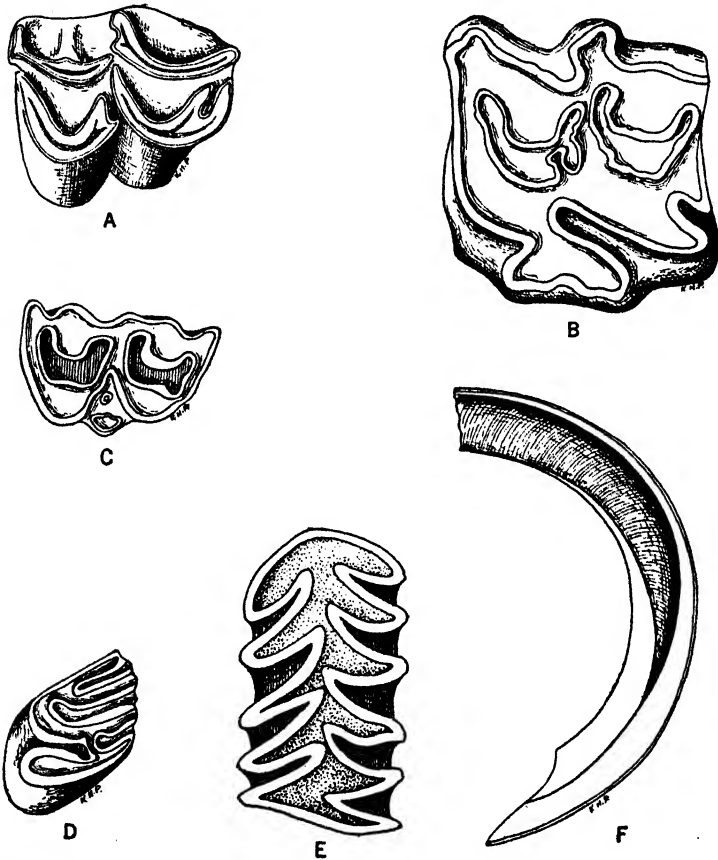


FIG. 83. Mammalian teeth. *A*, upper molar of moose; *B*, upper molar of horse; *C*, upper molar of cow; *D*, upper molar of beaver; *E*, first molar in lower jaw of muskrat; *F*, sagittal section of incisor of squirrel showing pulp cavity.

of different types are studied in position, it is seen that those with pointed cusps or with shearing edges must have an exact meeting of the opposing parts to make them effective and to avoid undue wear or breakage of the teeth. In a typical carnivore dentition, such as the dog's, this intermeshing of the parts is seen in its perfection. In this carnivorous type, there is practically no lateral movement, and this

lack of lateral movement is assured by the type of the connection between mandible and the skull. The condyle of the mandible in these forms is a modified cylinder, and the glenoid cavity is made reciprocally in cylindrical form by the building up of the edges so that there is little or no possibility of lateral movement. Specimens are sometimes found in which it is necessary to break the edges of the glenoid cavity to remove the mandible from the skull. Herbivorous mammals depend on a free movement of their jaws for chewing their food. The opposing surfaces of the condyle of the lower jaw and the glenoid cavity of the skull are flattened, as in the cow, allowing the teeth to be used in an antero-posterior, as well as a lateral, movement.

CHAPTER SEVEN

Axial Skeleton

The skeleton is one of the most interesting parts of the vertebrate body, since it is intimately associated with every activity of the animal. This framework can be understood only in the light of a knowledge of the long series of changes through which the vertebrate animals developed—changes which have left indelible impressions on the bones, either in the embryo or in the adult. The musculature has been most closely associated with the development of the skeleton, but the nervous and vascular systems also have had their effects and left their marks on the bones. The skeleton is about all that remains of the animals of past ages, but fortunately it contributes greatly to our knowledge of the fossil forms because of its many indications of the softer materials that have not been preserved.

The chief embryological source of bone is the mesoderm. The greater part of the skeleton is first formed in cartilage and is later transformed by a series of changes through which it becomes real osseous material with a characteristic structure. A second type, the membranous or dermal bone, is formed in a different way and may not go through a cartilaginous stage. Originally the membranous bone is on the outside of the body and developed from the corium. In higher forms these two types of bone are closely joined, and their origin can be determined only by a study of their embryonic development.

Cartilage was thought to be more primitive than bone because it appears first in the embryo and is the sole skeletal substance, except the notochord, in the lowest living vertebrates. However, paleontological evidence (Romer, 1942) indicates that bone was present in the oldest fish-like fossils known. Bone was common in the ostracoderms and acanthodian sharks (Fig. 11) which preceded the cartilaginous sharks. Cartilage is probably as old as bone but was present in the earliest vertebrates as an embryonic substance. Apparently bone arose very early in the history of the vertebrates, and the presence of cartilage in adults of many later vertebrates, such as sharks, sturgeons, and *Polyodon* (Fig. 14), is because these fishes have lost or failed to develop their bony structures and have retained their embryonic cartilage. A

series of skeletal structures showing progressive changes from cartilage to bone may be built up by selecting certain species of modern fishes, but, actually, it is highly probable that such a series would not represent the true historic stages of the development of cartilage and bone.

For convenience the skeleton is divided into regions: the axial skeleton, consisting of the skull, vertebral column, and ribs; the visceral skeleton, including all parts of the branchial arches; and the appendicular skeleton, consisting of the appendages and their girdles.

Skull

The skull has always been an intriguing subject for the anatomist. It is the most intricate unit in the skeletal system of the higher vertebrates. Since it first appeared, it has undergone a series of radical changes fusing certain elements and adding others from the skin and the visceral skeleton.

In the lower chordates without a skull such as *Amphioxus* (Fig. 7), the sense organs and anterior end of the central nervous system are not highly developed and have no skeletal protection. In the vertebrates these structures including the mouth become highly developed, and a skull is formed, enclosing and protecting them. In the lowest living vertebrates, the skull is a chondrocranium, a cartilaginous case enclosing only the brain, and is formed from the surrounding mesodermal tissues. This structure forms at the anterior end of the notochord and partly incorporates the tip of the notochord. In *Amphioxus* the notochord extends to the tip of the snout, but in the vertebrates the embryonic notochord extends only part way into the head, reaching the anterior edge of the otic or ear region.

The skull of the higher vertebrates is derived from three sources: (1) the chondrocranium or neurocranium, (2) the dermocranium, (3) the splanchnocranium (Fig. 85). The chondrocranium or neurocranium is the original structure surrounding the brain and is composed of cartilage which may be replaced in later development by chondral bone. The dermocranium consists of an outer covering of membranous bone formed from fused scales in the dermis or corium of the skin and which often becomes incorporated with the chondrocranium. The splanchnocranium is the endoskeletal elements of the visceral skeleton originally supporting the gills and becoming part of the skull of higher vertebrates. Although chondral in origin, part of the bones of the visceral skeleton become sheathed and replaced by membranous bones. These major skull units are more or less separate elements in many lower vertebrates, but they are incorporated into a single skull unit in the higher vertebrates. It is only by a comparative study of the skulls of the lower vertebrates and their embryology

that the origin of many bones in the skull of the higher vertebrates can be determined.

A comparative study of the successive classes and their skulls shows a progressive series of developments, many of which have been accompanied by changes of function. The shift from water to land life was accompanied by a release of a number of parts of both the skull and the visceral skeleton from their function of supporting the gills, and these elements became modified and used for other purposes. In tracing the history of the skull through the vertebrates, these changes will be considered in their proper place and sequence.

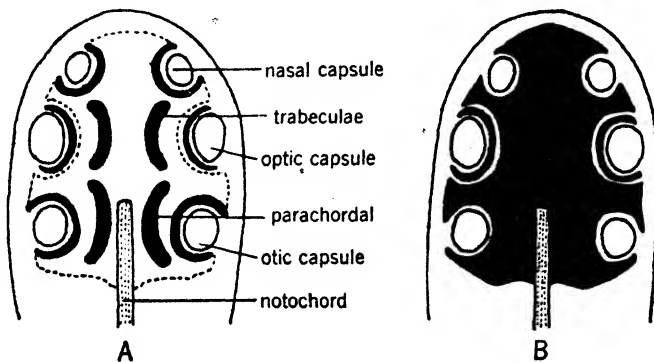


FIG. 84. Diagram illustrating embryological development of the chondrocranium; A, first stage of cartilage formation; B, latter stage of cartilage formation, covering floor and sides.

History and Development of the Skull

The embryological development of the skull (Fig. 84) starts with the formation of bars of cartilage: the parachordals, a pair that parallel the notochord and extend one on either side to the anterior end of the otic capsules; and the trabeculae, a pair anterior to the parachordals and extending to the anterior ends of the eyes. Capsules of cartilage also form about the sense organs, the ear (otic capsule), the eye (optic capsule), and the nose (nasal capsule). These cartilages coalesce forming the chondrocranium. The optic capsule remains free from the rest of the skull and enters into the formation of the eye (Fig. 84). Sclerotic bones may develop in the eyes but do not join the skull except in a few birds (owls). In vertebrates above the Chondrichthyes, ossification more or less replaces the chondral elements with bone. Dermal or membranous bones, originating as plates in the skin, cover and sheath the chondral elements. In all higher vertebrates, the dermal elements become deeply imbedded and incorporated with the ossified chondral elements. The visceral skeleton also appears as cartilage and assumes

its adult position with the rest of the skull. Some of the cartilages ossify and others are replaced by dermal bones.

The steps of skull formation, as seen in the embryological development of the higher vertebrates, can be traced in the skulls of the vertebrates, from the cyclostomes through the shark to the mammal. This is probably not the evolutionary sequence, as paleontology shows that the bony dermal skull, which appears late in embryological development, really appeared early in the history of the vertebrates.

The most primitive skull among living vertebrates is the imperfectly roofed cartilaginous neurocranium of the cyclostomes. No bone or dermal plates are present. The visceral skeleton of the cyclostome has little relation to the skull and is in the form of a modified branchial basket, which is probably a modern specialization of the primitive visceral skeleton.

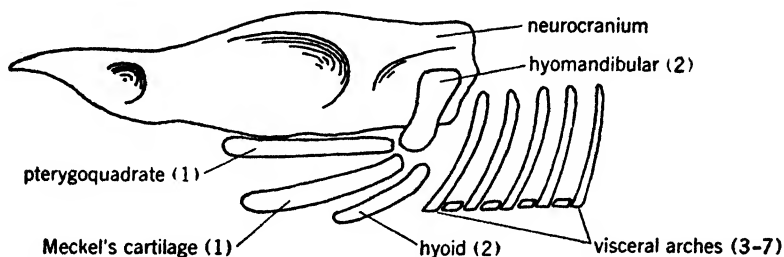


FIG. 85. Diagram of skull of shark showing relation of the visceral arches to the neurocranium.

The next step is seen in the elasmobranchs where the skull consists only of a chondrocranium or cartilaginous neurocranium (Fig. 85), which completely encloses the brain and has begun to incorporate the first two arches of the visceral skeleton. The first arch has divided; the upper half forms the upper jaw (pterygoquadrate or palatoquadrate cartilage), and the lower half forms the lower jaw (Meckel's cartilage). These are bound by ligaments to the neurocranium, and the mandible articulates on the palatoquadrate. The second arch divides to form a pair of dorsal hyomandibular cartilages and a lower hyoid series, which lose their gill function and lie close behind the jaws. The hyomandibular tends to shift forward and aid in supporting the jaw. These two arches thus start an addition to the skull and form the splanchnocranium, which becomes a very important part of the skull in higher vertebrates.

The more primitive Osteichthyes such as the gars, sturgeons (Figs. 86, 91), and *Amia* (Fig. 90) show several progressive steps in skull formation. The posterior end of the palatoquadrate cartilage separates

off as the quadrate, which articulates with the lower jaw and becomes suspended from the neurocranium by the hyomandibular. In these ganoid fishes numerous dermal plates of bone, derived from fused scales, appear as they did in the early Osteostraci and Placodermi (Fig. 8), from which they were probably inherited. These bony plates form an external skull or dermocranium, sheathing the neurocranium and the splanchnocranium. Many of these dermal plates can be homologized with skull bones of higher vertebrates. Sturgeons (Fig. 86) demonstrate a somewhat earlier stage of skull development, as the cartilaginous neurocranium, although encased in dermal bone, is a

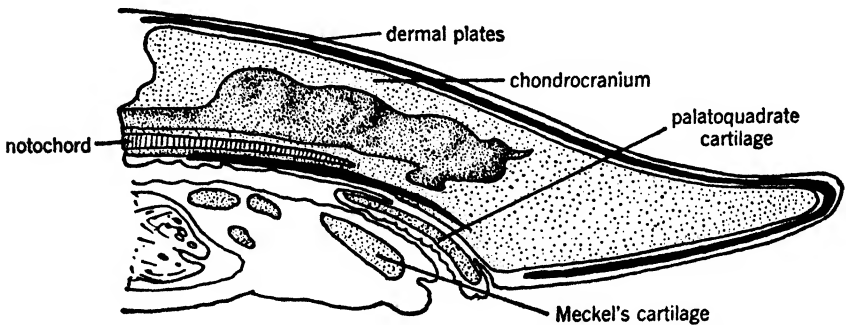


FIG. 86. Sagittal section through head of sturgeon. Dermal bones in black, cartilage in stipple.

tight, homogeneous structure as in the sharks. In gars and *Amia* (Fig. 90), the neurocranium shows a more advanced stage, as centers of ossification appear throughout the structure. This same type of skull is found in the ancient crossopterygians and was passed on to the labyrinthodont amphibians, although it may have been more ossified than in some of their present descendants. The teleost fishes also inherited this same type of skull but apparently ossified most of the chondral elements, which were united with the dermal elements, forming a single skull of double origin. The ossified end of the palatoquadrate became the quadrate bone, connected to the skull by the hyomandibular and forming the articulation for the lower jaw. The lower jaw is now largely of dermal plates formed about the Meckel's cartilage, which ossifies at the ends to form the articulars.

The amphibians, inheriting their skull from the crossopterygians, tend to retain the neurocranium as a more or less ossified chondrocranium, sheathed with dermal bones. In the transition, they soon lost the opercular bones and shifted the hyomandibular into the ear to become the stapes or columella auris. The quadrate, supporting the lower jaw, now is joined to the neurocranium.

The reptiles inherited their skull from the ancient amphibians and at first retained a number of primitive elements. They soon ossified all the chondral elements and lost all traces of the opercular bones. Several dermal and chondral elements, which modern amphibians do not develop at all, became conspicuous parts of the reptilian skull. Birds inherited the reptilian skull and made few changes.

Mammals inherited a skull that had already started to reduce and change bones in the Therapsida (Fig. 108). The quadrate and the articular moved into the ear to become the incus and malleus. The other small bones of the mandible disappeared, leaving only the dentary as the mandible. The dentary articulated against the dermal squamosal, which fused with a number of other bones to form the temporal on the side of the neurocranium. The number of bones has become reduced; some have been lost; and many fused with other elements.

Bones of the Skull

Chondral Elements

A review of the bones of the skull according to their origin is important, although it involves some repetition. It is possible to trace the skull bones of modern vertebrates from the three primitive origins: the chondral neurocranium, the dermocranium, and the visceral arches. Only the posterior end, lateral walls, and the floor of the chondral neurocranium ossify and give rise to bones in the higher vertebrates. Any portion of the chondrocranium remaining open or unossified in embryological development tends to be covered by dermal bones.

The posterior end or wall of the chondrocranium gives rise to the following bones: The unpaired *basioccipital* arises below the foramen magnum; the paired *exoccipitals* arise on each side of the foramen magnum; the unpaired *supraoccipital* arises above the foramen magnum and in the mammals (Fig. 87) incorporates dorsally a pair of dermal interparietals or postparietals. All four occipitals appear in the bony fishes although all may not ossify in some. They appear in all tetrapods except in the modern amphibians where only the exoccipitals ossify. All four bones fuse into an occipital bone in adult mammals. The floor of the chondrocranium gives rise to the following bones. The median unpaired *basisphenoid* (Fig. 87) develops just anterior to the basioccipital. It is present in a few fishes and extinct amphibians but becomes a prominent bone in the higher tetrapods. The median unpaired *presphenoid* develops just anterior to the basisphenoids. If the floor of the chondrocranium fails to close, as in the teleosts, a dermal *parasphenoid* forms in place of the basisphenoid

and presphenoid. In some reptiles and in mammals, a partial closure allows the chondral elements to form, so that a reduced parasphenoid may be present.

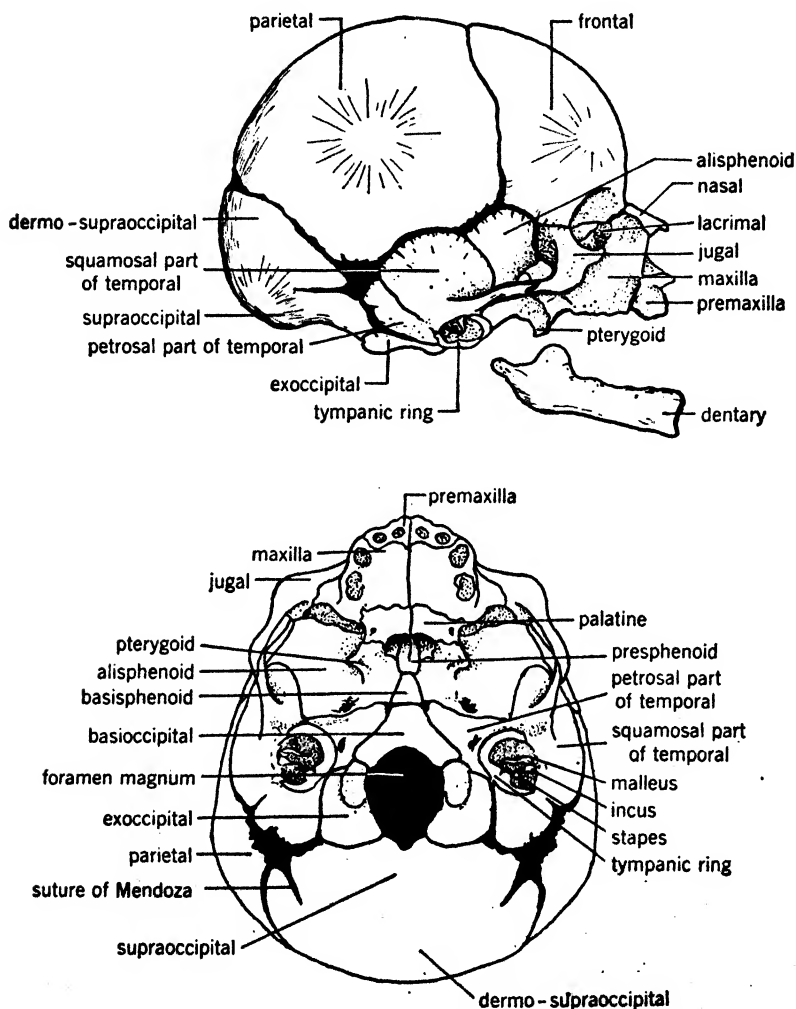


FIG. 87. Lateral and ventral view of skull of newborn human.

The *mesethmoid* is a median bone arising at the anterior end of the chondrocranium. Foramina for olfactory nerves usually pass through this bone. *Ectethmoids* occur lateral to the mesethmoid of many teleost fishes and are probably incorporated in the turbinals of higher vertebrates.

The optic capsule never becomes incorporated with the rest of the chondrocranium and consequently does not contribute to the skull.

It takes part in the formation of the sclera of the eye and frequently forms small plates of bone known as the *sclerotic bones*. The region of the orbit, in the side walls of the chondrocranium, gives rise to a number of paired bones. The *pleurosphenoids* arise in the orbit of bony fishes but are absent in many. They are commonly called alisphenoids but they are not homologous to the mammalian alisphenoid. They are placed laterally to the basisphenoid of reptiles and birds. The mammalian alisphenoid is apparently the epipterygoid of the reptiles. The *orbitosphenoids* originate in the orbits of bony fishes and, in some extinct amphibians and reptiles, and in living frogs, tend to fuse with the presphenoid, forming the *sphenethmoid*.

The otic or ear capsule of the chondrocranium gives rise to at least five paired elements, which are clearly defined in the teleosts. Some of these fail to ossify in the amphibians and other tetrapods. The otic series consist of the *prootic*, *epiotic*, and *opisthotic*, all of which fuse together to form the periotic or petrosal bone of mammals (Fig. 87), a part of the temporal bone. It is possible that two other elements, the *pteros* and *sphenotics*, may be included in the composite temporal bone of the mammals but are present as independent units only in bony fishes (Figs. 92, 93, 94).

The visceral or gill arches are chondral elements, the first two forming a part of the skull in most vertebrates. These elements, and the dermal bones accompanying them, form what is usually termed the splanchnocranium. The cartilages derived from the first visceral arch are the palatoquadrate or pterygoquadrate of the upper jaw, and the Meckelian cartilage of the lower jaw. Meckel's cartilage is present in all gnathostome vertebrates, although it is an embryonic structure in the higher forms. The second visceral arch gives rise to two sets of cartilages, the upper ends forming the hyomandibular cartilages and the lower portion forming the hyoid cartilages.

The paired *articulars* ossify from the proximal ends of Meckel's cartilage and form the articular surfaces of the lower jaw in bony vertebrates, with the exception of the mammals, where it has been taken into the middle ear as the malleus. The only other part of the Meckelian cartilage to ossify is the median portion, which may form a small mentomeckelian structure, as in amphibians.

The paired *quadrates* ossify from the posterior end of the palatoquadrate cartilage and appear as separate bones early in the history of the Osteichthyes, where they are suspended from the hyomandibular and articulate with the articulars. The quadrate forms the articulation for the lower jaw in all higher vertebrates except the mammals, where it has been taken into the middle ear as the incus.

The *epipterygoids* of some extinct amphibians and reptiles appear

as an ossification of a dorsal orbital process of the palatoquadrate cartilage. In mammals it becomes a part of the wall of the orbit and is known as the alisphenoid.

The *metapterygoid* (paired) is the only other bone to form from the palatoquadrate cartilage, and this bone appears in fishes only. The other pterygoids are dermal. Romer (1945) refers to this bone as synonymous with the epipterygoid.

The *hyomandibular* (paired) appears in the Osteichthyes, ossifying from the hyomandibular cartilage, derived from the dorsal part of the second visceral arch, and becomes a prominent bone extending from the neurocranium to the quadrate. In the land vertebrates it unites with another element to form the columella auris or ear bone of the amphibians, reptiles, and birds. The hyomandibular portion, usually referred to as the stapes, is the only part retained by the mammals, where it becomes the small stapes of the middle ear.

The *symplectic* (paired) (Fig. 92) is a small bone appearing in the Osteichthyes along side of the distal part of the hyomandibular and apparently derived from the hyomandibular cartilage. It is typically a bone of fishes, and its fate in the tetrapod is uncertain. Some think it is combined with the hyomandibular to form the columella auris.

Dermal Elements

The large number of dermal plates present on the skull of the early Osteichthyes were probably inherited from earlier placoderms. The crossopterygians retained many of these and passed them on to the ancient amphibians, which in turn passed them on to the early reptiles. Modern teleosts received their share and incorporated many with the chondral elements to form the modern fish skull. Tetrapods lost some, but retained others, either as independent units or fused with chondral elements. In the embryo, the chondral skull forms first, and, wherever it does not cover the brain, the dermal bones may assume the covering function. Furthermore many of the chondral elements, particularly those of the visceral skeleton or splanchnocranium, are sheathed with dermal bone. .

The major dermal bones forming the roof of the skull, which in the higher vertebrates is left open by the chondrocranium, are as follows:

The paired *parietals* appear as a pair of large plates posteriorly, and are present in all vertebrates possessing dermal bone. In some fishes, the bones formerly called frontals are now recognized as parietals, and the large bones, formerly called parietals, are now called postparietals.

The paired *frontals* are large dermal plates arising just anterior to the parietals and are present in all vertebrates above the Chondrichthyes. They may fuse as in the adult human.

The paired *nasals* are usually more or less elongated dermal bones anterior to the frontals, and over or between the nares. They are present in all vertebrates above the Chondrichthyes.

Postfrontals, *prefrontals*, *postparietals*, and many minor dermal bones appear in the roof of the skulls of fishes and are retained in many of the extinct amphibians and reptiles, some still appearing in modern reptiles. The postparietals fuse with the mammalian supraoccipital to form the dermal part.

The paired *lacrimal*s appear anteriorly on the sides of the skull of fishes and are present in all tetrapods, where they are usually penetrated by the lacrimal duct.

On the sides of the skull many dermal bones appear covering the chondral elements of the splanchnocranium.

The *squamosals* (paired) are dermal bones on the side of the skull and appear first in bony fishes, although they are not present in all. They become prominent bones in the reptiles and form the upper part of the mammalian temporal (Fig. 87).

On the sides of the paired palatoquadrate cartilages in the primitive bony fishes, the dermal *premaxilla*, *maxilla*, *jugal*, and *quadratojugal* appear and in the tetrapods form the major portion of the upper jaw, except in mammals where the quadratojugal disappears and the jugal becomes the zygomatic or cheek bone.

The skin of the roof of the mouth of primitive bony fishes gives rise to paired *prevomers*, *endopterygoid*, *ectopterygoids*, *palatines*, and the unpaired *parasphenoid*. The fused prevomers form the bone formerly called vomer of the fishes and lower tetrapods. The mammalian vomer is probably derived from the parasphenoid. The endopterygoids form the pterygoid bones of the tetrapods and, in mammals, become a pair of processes posterior to the palatine. The ectopterygoids, present in the higher fishes, reappear as the transpalatines in the roof of the mouth of the reptiles. They may be fused with the endopterygoids to form the pterygoid process of the mammals. The palatines are common bones in the roof of the mouth of most of the higher vertebrates. The parasphenoid appears in those vertebrates that fail to fuse the chondral elements in the floor of the chondrocranium. It is a prominent bone in the floor of the brain case of most bony fishes and amphibians. In mammals it is thought that it forms the unpaired bone commonly called the *vomer*, since the so-called vomer of fishes arises as a paired structure which may be called *prevomer* to eliminate confusion.

TABLE OF THE COMMON SKULL BONES IN THE FIVE CLASSES OF VERTEBRATE

	Regions	Names of bones	Osteichthyes	Amphibia	Reptiles	Birds	Mammals	Remarks
Cranial Elements	Nasal	D lateral ethmoid	+	+	+	+	+	Vomers variable in mammals; may be parasphenoid.
		<i>nasal</i>	+	+	+	+	+	
		D mesethmoid*	+	+	+	+	+	
		<i>vomer</i> (prevomer)	+	+	+	+	+	
		D septomazillary		+				
	Frontal	D frontal	+	+	+	+	+	These bones are usually joined with the alisphenoids in mammals to form a single bone, the sphenoid.
		<i>prefrontal</i>	+	+	+	+	+	
		D postfrontal	+	+	+	+	+	
		<i>lacrimal</i>	+	+	+	+	+	
		<i>supraorbitals</i> (v)	+	+	+	+	+	
		<i>suborbitals</i> (v)	+	+	+	+	+	
		<i>postorbitals</i>	+	+	+	+	+	
		<i>sclerotics</i>	+	+	+	+	+	
		<i>orbitosphenoid</i>	+	+	+	+	+	
		<i>presphenoid</i> *	+	+	+	+	+	
	Parietal	basisphenoid	+	+	+	+	+	Fused with parasphenoid in birds.
		pleurospenoid	+	+	+	+	+	Joined with frontal in <i>Rana</i> . Usually fused with adjacent bones.
		D parietal	+	+	+	+	+	
		<i>interparietal</i>	+	+	+	+	+	
		sphenotic	+	+	+	+	+	Fused with supraoccipital in mammals.
	Ear	pteric	+	+	+	+	+	
		prootic	+	+	+	+	+	
		opisthotic	+	+	+	+	+	
		D squamosal	+	+	+	+	+	Fused in mammals to form temporal.
	Occipital	supraoccipital	+	O	+	+	+	Often has an added dermal element.
		exoccipital	+	+	+	+	+	
		basioccipital *	+	O	+	+	+	
	Palatal	D palatine	+	+	+	+	+	Pterygoid of tetrapods. Probably fused with the pterygoid of mammals. Transpalatine of reptiles.
		D endopterygoid	+	pt	pt	pt	pt	
		D ectopterygoid	+	+	+	+	+	
		D parasphenoid*	+	+	+	+	Vo	Vomer of mammals.
Visceral Elements	Upper jaw	D premaxilla	+	+	+	+	+	Incus of mammals. Alisphenoid of mammals, metapterygoid of fishes.
		<i>maxilla</i>	+	+	+	+	+	
		<i>jugal</i>	+	+	+	+	+	
		<i>quadratojugal</i>	+	+	+	+	+	
		quadrate	+	+	+	+	+	
		epipterygoid	+	+	+	+	+	

Cartilage bones in bold-faced type; membranous bones in italics.

* Median single bones.

(v) = variable in number.

O = not ossified.

† Presence is uncertain or present only in extinct forms.

TABLE OF THE COMMON SKULL BONES IN THE FIVE CLASSES OF VERTEBRATES (Contd.)

	Regions	Names of bones	Osteichthyes	Amphibia	Reptiles	Birds	Mammals	Remarks
Visceral Elements	Lower jaw	<i>dentary</i>	+	+	+	+	m	Mandible of mammals.
		<i>coronoid</i>	+	+	+	+		
		<i>splenial</i>	+	+	+	+		
		<i>angular</i>	+	+	+	+	ty	Tympanic.
		<i>surangular</i>	+	+	+	+		
		<i>articular</i>	+	+	+	+	m	Malleus of mammals.
	Hyoid arch	<i>hyomandibular</i>	+	st	st	st	st	Stapes of tetrapods.
		<i>symplectic</i>	+	+	+	+	+	
		<i>interhyal</i>	+	+	+	+	+	
		<i>epihyal</i>	+	+	+	+	+	These five bones are part of the hyoid series of tetrapods.
		<i>ceratohyal</i>	+	+	+	+	+	
		<i>hypohyal</i>	+	+	+	+	+	
		<i>basihyal</i>	+	+	+	+	+	
	Gill covers	<i>preopercular</i>	+	+				†Ichthyostegalia.
		<i>opercular</i>	+					
		<i>subopercular</i>	+					
		<i>interopercular</i>	+					

Fishes above the Chondrichthyes develop a group of flat dermal bones in the operculum covering the gills. These are the *opercular*, *preopercular*, *subopercular*, and *interopercular* (Figs. 94, 125). These typical fish structures serve to protect the gills. They are lost in tetrapods, although the Ichthyostegalia and a few other early amphibians (*Palaeogyrinus*) retain a preopercular (Fig. 100).

The lower jaw, originally formed of Meckel's cartilage, becomes sheathed with paired dermal plates which reach their greatest number in some of the reptiles. The *dentary*, *splenial*, and *angular* are prominent dermal bones arising on the mandibles of fishes. Primitive fishes and amphibians and modern reptiles may have in addition a *surangular*, *postsplenial*, *coronoid*, and several others. The primitive mammals lost all but the dentary, although it is thought that the angular enters the ear region to form the tympanic ring, a bone supporting the tympanic membrane and incorporated in the temporal bone. In many mammals a tympanic bulla is formed, which, at least in part, is a growth from the tympanic ring. In mammals the entire lower jaw is formed of a single pair of bones, the dentaries. These are often fused in the adult.

Ventral to the jaws, a series of slender bones, the *branchiostegals*, develop and support the gill membranes or lower part of the operculum of fishes. These articulate on the ceratohyal of the hyoid structure and are confined to the Osteichthyes.

*Fish Skull***Shark Skull**

The skull of the sharks is a cartilaginous chondrocranium (Fig. 126) which serves as the permanent skull. The visceral arches have contributed the upper and lower jaws and their attachments to the skull (Figs. 85, 88).

The visceral skeleton (Fig. 88) of the shark usually consists of seven pairs of arches, the first pair being used for the jaws, the second for the supporting arch, and several vestigial cartilages of uncertain origin being associated with the mandibular arch. A few sharks, such as *Heptanchus* and *Hexanthus*, have more than the normal number.

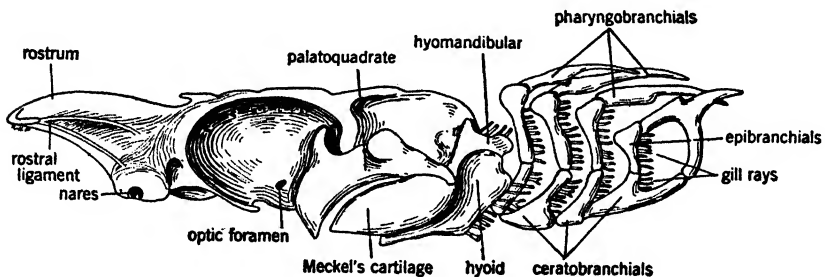
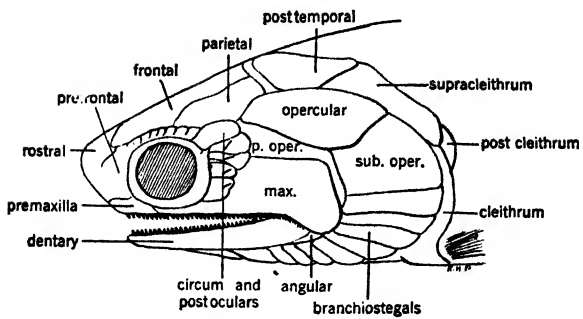


FIG. 88. Chondrocranium and visceral arches of a shark (*Squalus acanthias*). After Wells.

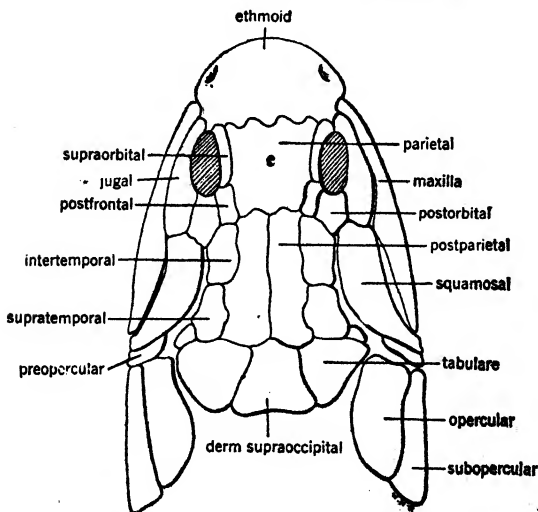
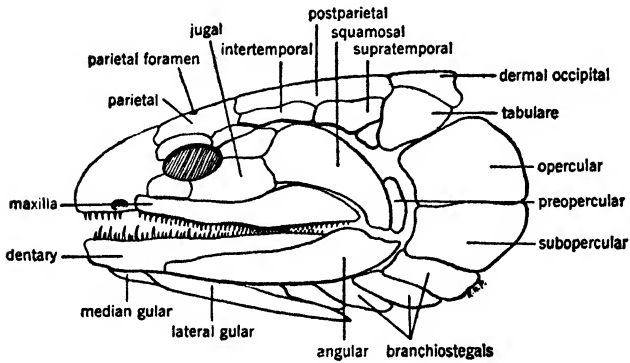
The mandibular arch is a U-shaped structure, which is joined to the skull by means of the second or hyoid arch. Five branchial arches, each with a gill, are attached to this ventral median, hyal series. In sharks, the branchial arch consists of four or more pieces, a ventral basibranchial forming the connecting element.

There are numerous openings in this chondrocranium, such as fontanelles and smaller foramina, passageways for nerves and blood vessels. Many of these foramina persist throughout the vertebrates and are generally homologous. The future ossifications are fixed somewhat by these foramina as well as by points at which movement is possible.

The chondrocranium of the shark is an irregular, plowshare-shaped mass of cartilage with numerous openings but with no sutures. It surrounds the brain completely. The capsules of the nose and ears have joined with the rest of the mass, but the capsules of the eyes remain free and are able to move. A median prolongation, the rostrum, with the two nasal capsules attached laterally at the base, marks the anterior end. The nasal cartilages are delicate and have openings for the nostrils. Posterior to the rostrum, the cartilage extends out laterally



Skull of *Palaeoniscus*, a fossil chondrosteian. After Goodrich.



Skull of *Osteolepis*, a fossil crossopterygian. After Goodrich.

FIG. 89. Skulls of early bony fishes.

to form the preorbital ridge, and a similar ridge is developed as the postorbital. The posterior end of the chondrocranium, which includes the otic capsules, is heavy and substantial. The ventral region is much narrower and more irregular with a keel on the ventral side of the

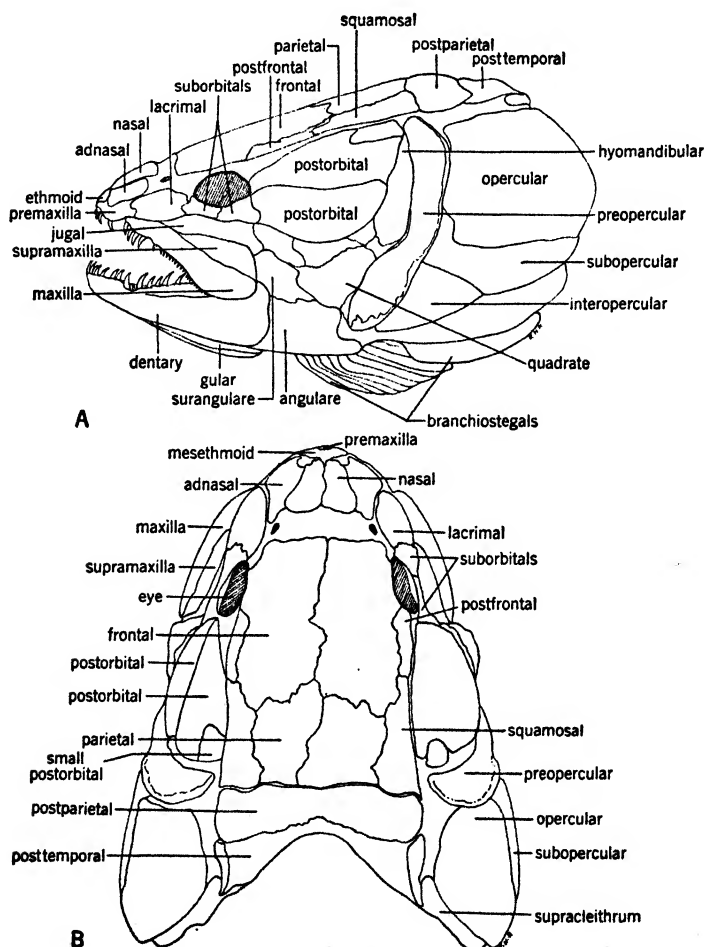


FIG. 90. Skull of *Amia calva*. A, lateral; B, dorsal.

rostrum. The region ventral to the brain is quite narrow between the otic capsules. The sella turcica, a depression on the floor of the chondrocranium into which the hypophysis projects, shows plainly from the ventral side, in its usual position just posterior to the optic chiasma. The notochord shows as a light streak along the median line, extending forward to the anterior border of the otic capsules. The dorsal side of the chondrocranium has a pair of large anterior fontanelles formed

by the trough-shaped rostrum, and, ventrally, another pair of openings that lead to the brain cavity. The epiphyseal foramen for the pineal body, which lies just posterior to the anterior fontanelles, is covered with a membrane.

Between the otic capsules is the endolymph fossa, into which the endolymph and perilymph ducts of the ears open. The foramen magnum, with its small condyle-like structures, marks the articulation with the vertebral column. Over the surface, at various points, are large and small foramina for nerves and blood vessels, those for the cranial nerves coming out laterally and ventrally. The chondrocranium of the shark encloses the brain and protects it from stresses and strains caused by the movements of the visceral skeleton. By the consolidation of the sense capsules with the rest of the skull, these parts receive additional protection.

Intermediate Fish Skull

The sturgeon (Fig. 86) retains the chondrocranium but also adds a number of bony dermal plates, representing coalesced scales. The dermal skull may be peeled off like a glove, revealing the unossified chondrocranium beneath. The dermal plates are external and are usually sculptured, thus showing their superficial position. The lateral line can be traced over these dermal elements by a series of small tunnels extending along its path. In many intermediate fishes (Figs. 90, 91), the series of dermal plates join and assume definite positions, thus approaching the conditions found in the teleosts. Several skull conditions may be traced through the intermediate series represented by fishes such as *Amia* (Fig. 90 A, B), *Lepisosteus*, *Acipenser* (Fig. 91), and *Polypterus*. In these there are different stages of ossification of the chondrocranium, with a gradual sinking in of the dermal bones; until they finally join closely with the chondral bones to form the skull of the teleosts. The first ossifications are always found around the sense organs and the foramina of the cranial nerves.

The lower jaw of *Amia* is covered with dermal plates: a large dentary, which sheathes the anterior end; and the articular, angular, and surangular, which cover the posterior end. There are several ossifications of the Meckelian cartilage. The inner surface is covered by the coronoid and splenial.

Teleost Skull

Some primitive teleosts, such as the trout and salmon, retain much cartilage in the chondrocranium, but the higher teleosts have a well-ossified skull.

Plates form around the sense capsules and enter into close relations with the ossifications of the chondrocranium. These plates complete the covering of the brain and build up a series of braces for the jaws. The higher teleosts have a fixed quadrate, braced by a series of bony elements that make powerful jaw action possible. By the complete ossification of the chondrocranium and the sinking in of the dermal

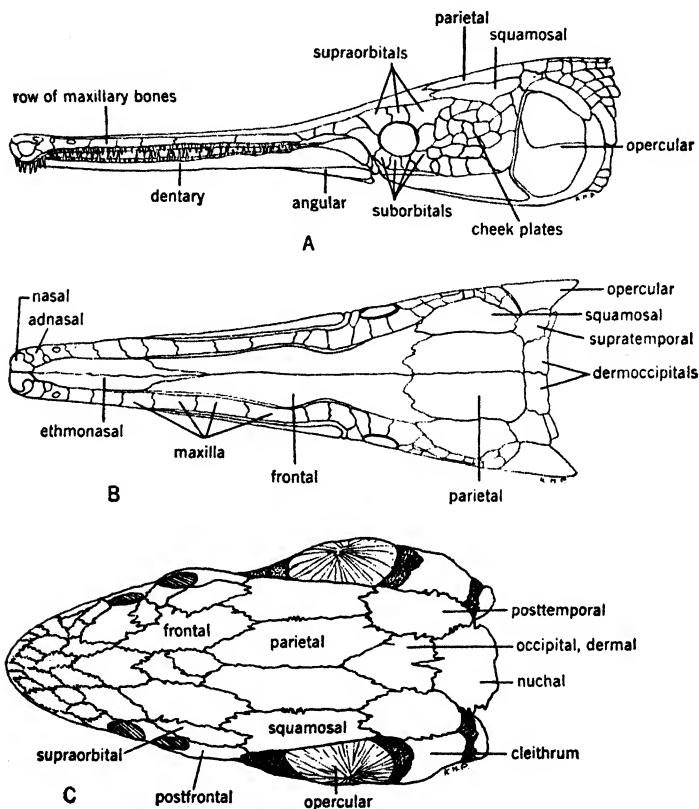


FIG. 91. Skulls of intermediate fishes. A, B, lateral and dorsal views of skull of gar (*Lepisosteus*), after Mayhew; C, dorsal view of skull of sturgeon (*Acipenser*).

bones to join with it, the skull of the teleost is formed. Each of the sense organs is surrounded by a series of bony elements for protection, so arranged as to permit some movement and freedom for growth. The brain thus becomes surrounded with a structure made up of separate bony elements, with fenestra and foramina to permit the entrance and exit of nerves, blood vessels, and other structures.

The branchial structures of the teleosts have been changed to bone or replaced by dermal elements. The lower jaw consists of several plates, the dentary, angular, and the articular, which is the ossified

end of Meckel's cartilage (Figs. 92, 125). Other bones may be present in the jaw, but generally the number is not large. The palatoquadrate is replaced by new bones in the formation of the upper jaw which became a brace for the quadrate. The new bones, of the upper jaw, the premaxilla, and maxilla, are of dermal origin and also articulate with the quadrate through some connecting element such as the jugal or zygomatic. The maxilla of the higher fishes does not bear teeth but serves to form support for the borders of the mouth.

The skull of the carp (*Cyprinus carpio*) represents a very complete ossification of the chondrocranium as well as a close interlocking of the

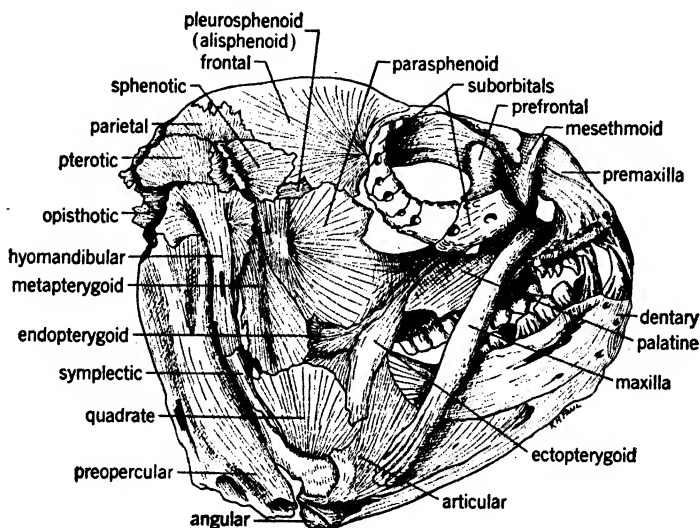


FIG. 92. Skull of *Anarrhichthys ocellatus*.

cartilaginous and dermal elements (Figs. 93, 94). The plan of the skull is fairly typical of that found in the teleosts, with the added advantage that the bones are quite solid and have very definite outlines and plain sutural lines. The brain case and sense organs are completely covered by a well-knit series of bones that form the neurocranium. The foramen magnum is surrounded by four occipital bones, one being dorsal (the supraoccipital), two lateral (the exoccipitals), and a single ventral (the basioccipital). The ear is surrounded by two bones, the prootic and the epiotic, the opisthotic probably being fused with the prootic. The pterotic and sphenotic are also present in the roof. The optic tract reaches the eye through a foramen in the orbitosphenoid. Sclerotic plates develop around the eye but are not connected with the skull. The lacrimal bone, in the anterior angle of the eye socket, merely represents the anterior element of the suborbital ring (Fig.

92), but it receives no duct from the eye. The nerves of the olfactory tract reach the nasal sacs through foramina in the ethmoid bone. The brain case is made up of the four occipital bones, the prootics,

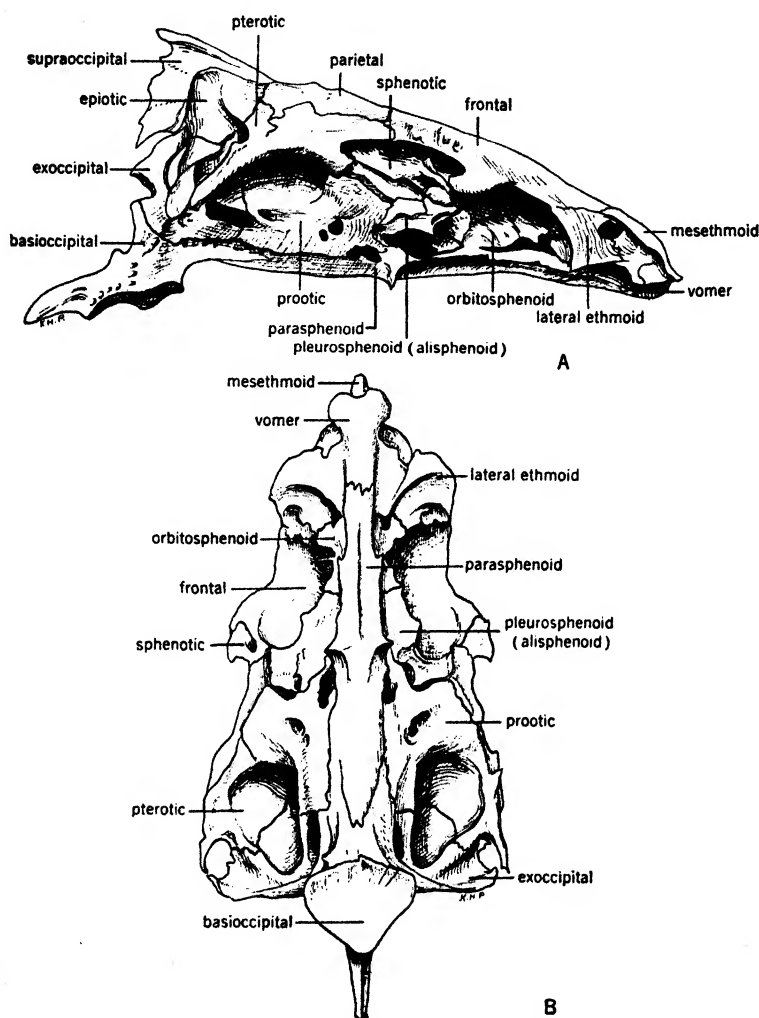


FIG. 93. Skull of carp with operculars and facial bones removed. A, lateral; B, ventral.

epiotics, pleurospenoids (alisphenoids), orbitosphenoids, and the single mesethmoid (Fig. 93 A). The floor is completed by the long dermal parasphenoid, which extends almost the complete length of the skull (Fig. 93 B). The vomer is applied to the ventral surface of the parasphenoid at its anterior end. The roof is made up of the supraoccipital,

prefrontals, frontals, postfrontals, supraorbitals, pterotics, and the mesethmoid (Figs. 92, 94). The rostral extends from the mesethmoid to the premaxillae, which are not toothed in the carp. The key element of the jaw series is the quadrate, which is braced to the roof of the skull through the symplectic and the hyomandibular (Fig. 94), the latter articulating with the pterotic and postfrontal. The quadrate is braced to the anterior part of the skull through the pterygoids and palatines. The metapterygoid (Fig. 94), a cartilage bone, fills in the gap between the quadrate and the hyomandibular, connecting with the palatines and filling in the pharyngeal region. A small ectoptery-

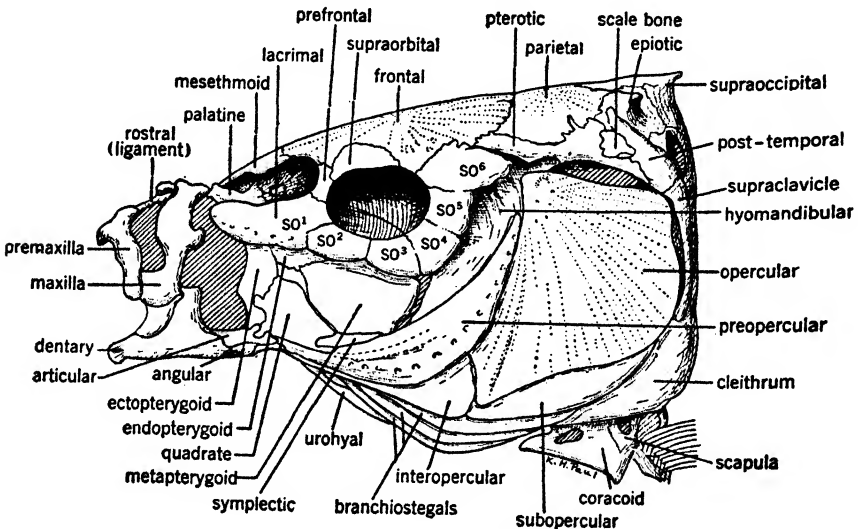


FIG. 94. Side view of carp skull, *Cyprinus carpio*. After Gregory.

goid is developed on the external edge of the palatoquadrate bar. The mandible (Fig. 110 A), also toothless, consists of a dentary, a small angular, and an ossified articular.

The opercular series, which covers the gill region, consists of four bones, the opercular, preopercular, subopercular, and interoperculars (Fig. 125). These bones cover the gill slits, so that the gill region is no longer exposed, as it is in the sharks. The opercular has a facet by which it articulates with the hyomandibular (Fig. 125).

The gills are connected with the skull through the hyal series consisting of the basi-, hypo-, cerato-, epi-, and interhyal (Fig. 127). The interhyal articulates with the hyomandibular, and the epihyal with the opercular. The entoglossal or urohyal, a modified branchiostegal, is a median bone articulating with the basihyal.

Each of the five gill bars, or branchials, consists of a number of ele-

ments: a basi-, hypo-, cerato-, epi-, and pharyngobranchial, the last at the dorsal end of the arch. The fifth arch is modified, its pharyngeal element being enlarged and highly specialized and supplied with pharyngeal teeth, which are rubbed against a horny pad (Fig. 127), on the basioccipital.

Amphibian Skull

The skull of the amphibian is inherited from its fish ancestors, retaining many of the skull elements but losing most of those directly connected with the branchial apparatus and gills. The shift from water to semi-land life left many of the fish elements without vital function. Accompanying this change the number of bones was much reduced.

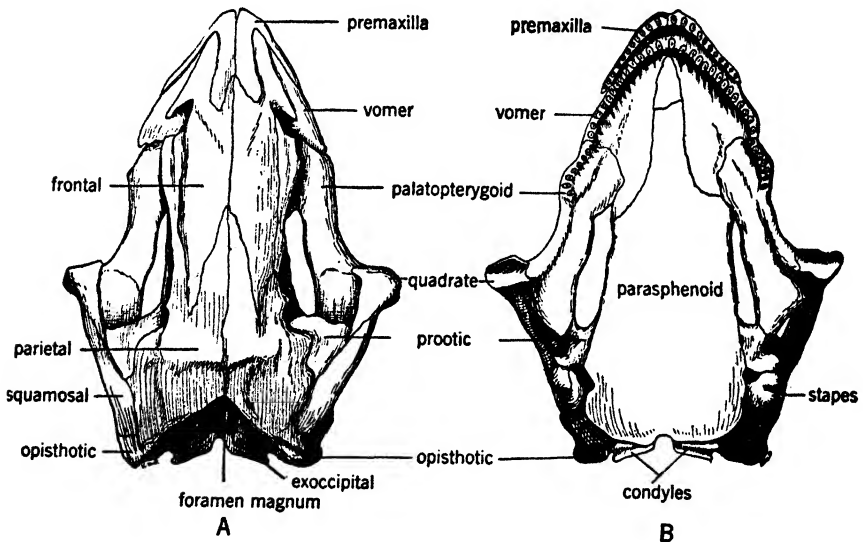


FIG. 95. Skull of *Necturus*: A, dorsal; B, ventral.

The skull of the earliest known amphibians, the *Ichthyostegalia* (Figs. 100, 101), retained numerous fish-like characteristics, and their skull structure is similar to those of the primitive fishes. The *Ichthyostegalia* had no openings on the dorsal side of the skull except those for the eyes and the pineal body, since the external nares opened on the ventral side in these animals. The later amphibians, such as *Eryops*, had the external nares on the dorsal side of the skull. The lateral lines and the distribution of the skull elements are decidedly fish-like, and comparison with the primitive fishes shows many similarities. The retention of the preopercular bone in the *Ichthyostegalia* marks the last appearance of any part of the gill cover in the tetrapods. The skull of modern amphibians (Figs. 95, 96, 97), is striking for its

compactness, in contrast to the loosely knit skull of most fishes. There is a great reduction of the number of bones, since many of the fish elements have been combined with others, changed in function, or entirely lost. This reduction is partly due to the retention of a chondrocranium that is not completely ossified. The jaws, instead of being loosely articulated to the sides of the skull as in fishes, appear to be an integral part of it. The nasal and oral regions are much simplified by the loss of many small elements. The quadrate is no longer articulated to the skull through the symplectic and hyomandibular, but through the squamosal. The hyomandibular has become the stapes, and the symplectic is thought to become the columella, forming a bone in the middle ear for transmitting sound vibrations. The skull is platybasic (flat-

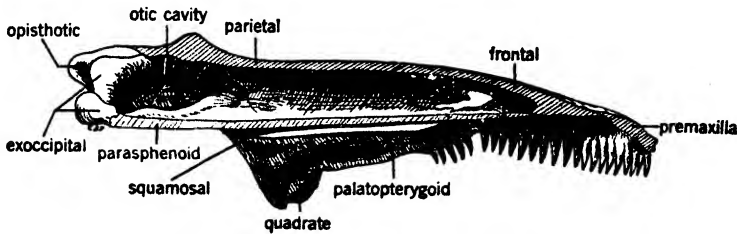


FIG. 96. Skull of *Necturus*, sagittal section.

tened), and the trabeculae, a pair of cartilaginous bars, paralleling the notochord in embryological development, meet in the region of the ethmoid plate. The two occipital condyles are formed by the exoccipitals. The neurocranium is quite narrow in the frog, being about one-sixth of the total width of the skull (Fig. 97 A, B). The foramen magnum is surrounded by the exoccipitals, as the other occipital bones are not ossified. Since so much of the chondrocranium is retained, the brain is surrounded mostly by cartilage. The nose is in a nasal capsule, having a septomaxillary developed in connection with it and also an external nasal bone. The orbitosphenoid is not ossified, and the optic nerve extends through a foramen piercing the cartilage (Fig. 96). The otic elements are peculiar in that only the prootic and opisthotic are present as separate bones. The stapes (Fig. 97 B) is well developed, and in anurans has its base in position in the foramen vestibuli and its columella in contact with the tympanum, which is supported by the cartilaginous annulus tympanicus (Fig. 97 A).

In the frog the roof of the skull (Fig. 97 A) consists of the frontoparietals, the nasals, and the ethmoids, with the prootics and sphenethmoids as side walls. The ventral part of the brain case is made up of the dagger-shaped parasphenoid and the triangular vomers, both of which are dermal bones. The splanchnocranium is extensive, and its

AXIAL SKELETON

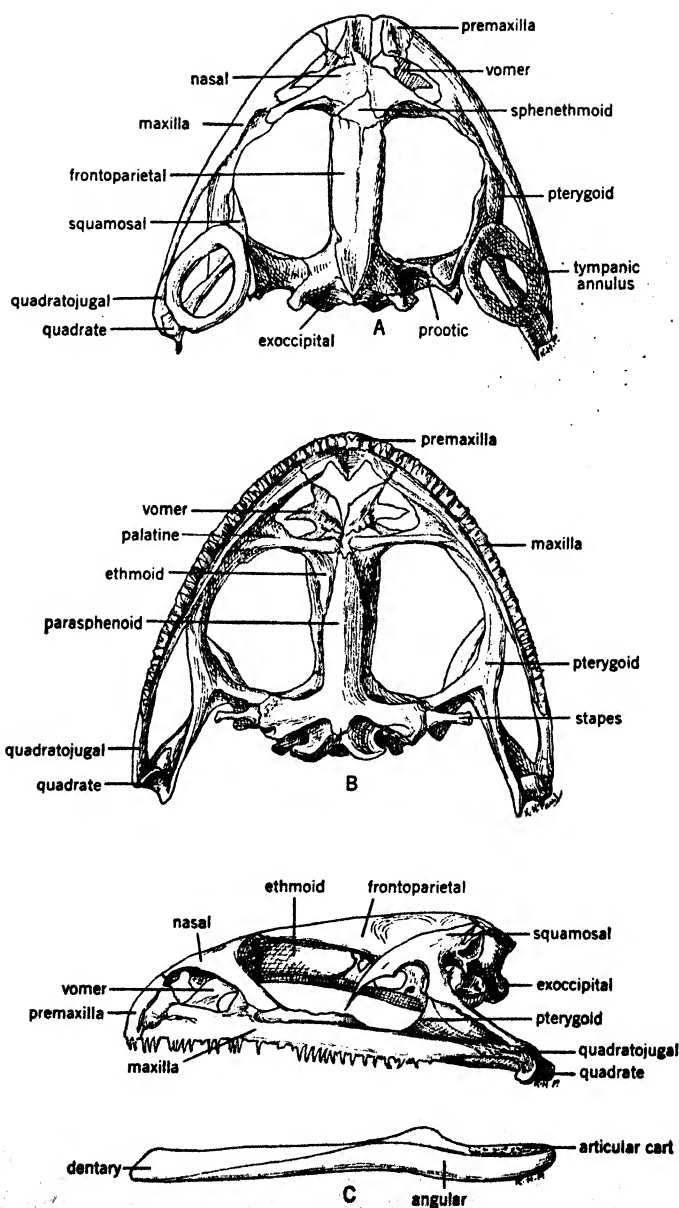


FIG. 97. Three views of the skull of *Rana catesbeiana* (bullfrog) A, dorsal; B, ventral; C, lateral.

outline gives width to the skull. The premaxilla, maxilla, and quadrato-jugal form the arc that extends to the quadrate. A large pterygoid forms the second brace for the arc, connecting with the palatine anteriorly and the prootic posteriorly. The vomer, premaxilla, and maxilla are toothed in *Rana*.

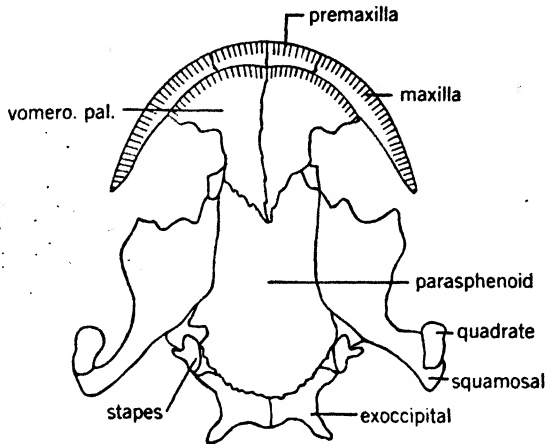


FIG. 98. Ventral view of skull of *Cryptobranchus alleganiensis*.

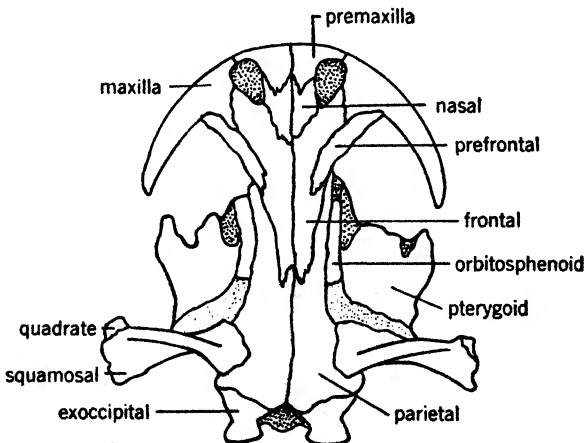


FIG. 99. Dorsal view of skull of *Cryptobranchus alleganiensis*.

The mandibular cartilage extends anteriorly from the dentary, forming the mentomeckelian cartilages. The bones of the mandible are the dentaries, articulars, and angulars, only the dentary being toothed (Fig. 97 C).

The visceral skeleton is much reduced in *Rana* but is more extensive in forms with permanent gills, such as *Necturus* (Fig. 128 A) and

Cryptobranchus, where it may show remains of four visceral arches posterior to the hyoid arch. The body of the hyoid is a cartilaginous plate formed by the fusion of the central parts.

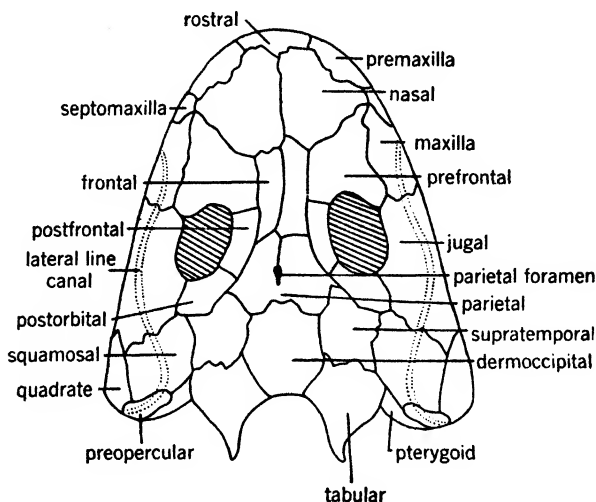


FIG. 100. Dorsal view of skull of *Ichthyostegalia*. Note the vestige of a preopercular which overlies the quadratojugal, squamosal, and pterygoid.

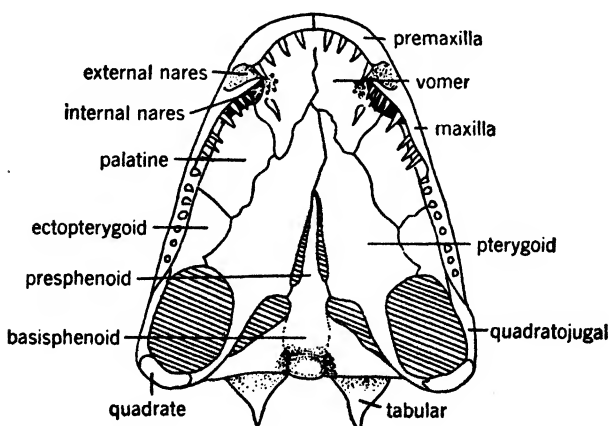


FIG. 101. Ventral side of the skull of *Ichthyostegalia*. To show the pattern of the palatal view of this primitive amphibian. Note the external nares on the ventral side in this animal.

The skull of a modern urodele, such as *Cryptobranchus* or *Necturus* (Figs. 95, 98), shows a decided reduction in skull elements, when compared with a labyrinthodont. Part of the chondrocranium has failed to ossify, some bones have dropped out, and others have been reduced

in size. There is a large, open area around the eye caused by the loss of small bones surrounding the socket in labyrinthodonts. The posterior limbs of the maxillae are not tied to the posterior part of the skull by the jugal or the quadratojugal. The median region of the skull roof is formed by the parietals, frontals, nasals, and premaxillae; the anterior lateral region is filled in by the prefrontals and maxillae. Posteriorly, the lateral area is filled in by the otics. An orbitosphenoid covers the side of the anterior brain-case region. The pterygoid is large and shows clearly on the dorsal side of the skull. The squamosal is prominent, extending out and covering the quadrate. The large parasphenoid and vomeropalatines form the greater part of the ventral side of the skull. The mandible of *Necturus* consists of a large toothed dentary, a toothed splenial, a cartilaginous articular, and an angular (Fig. 110 D, E).

Reptilian Skull

The skulls of modern reptiles are easily differentiated from those of the amphibians, but those of primitive reptiles and primitive amphibians are not so easily separated. Whereas modern reptiles are characterized by having a single condyle, the fossil Therapsida (Fig. 108) had two, as do the amphibians and mammals. The condition of the palate serves to separate modern reptiles and amphibians but not the older forms. In modern reptiles, the tropibasic condition of the skull is perhaps one of the most striking features; the trabeculae join each other in the region between the eyes, so that the skull is high rather than flat. Reptiles have a number of elements that do not appear in modern amphibians, such as the transpalatines and epipterygoids; and the parasphenoids (Fig. 107), so characteristic of both the fishes and amphibians, become small or vestigial. Some reptiles, particularly the turtles (Fig. 109), have a very heavy skull with bones closely joined, and the quadrate firmly fixed, a condition called monimostylic; others have lighter skulls in which the bones are not so closely joined and movement of the quadrate is possible, a condition known as streptostylic. Snakes and many lizards show this condition of a free quadrate. The skull of the reptile is a much better mechanical structure than that of the amphibians. Within the group there is much variation associated with different habitats and different food habits. The number of skull bones has been reduced through the dropping out or through the joining of separate elements. The sutures become stronger and better knit together; bracing gives the skull added strength, and there is a tightening up of the posterior part of the skull so that the quadrate is well braced, supporting a better lower jaw and making possible a stronger jaw musculature. All traces of the lateral line are lost, and

there is a freer movement of the skull on the atlas because of the type of condyle and improved cervical vertebra.

The classification of the reptiles is based partly on skull characters starting with the early cotylosaurs, in which the roof has no openings

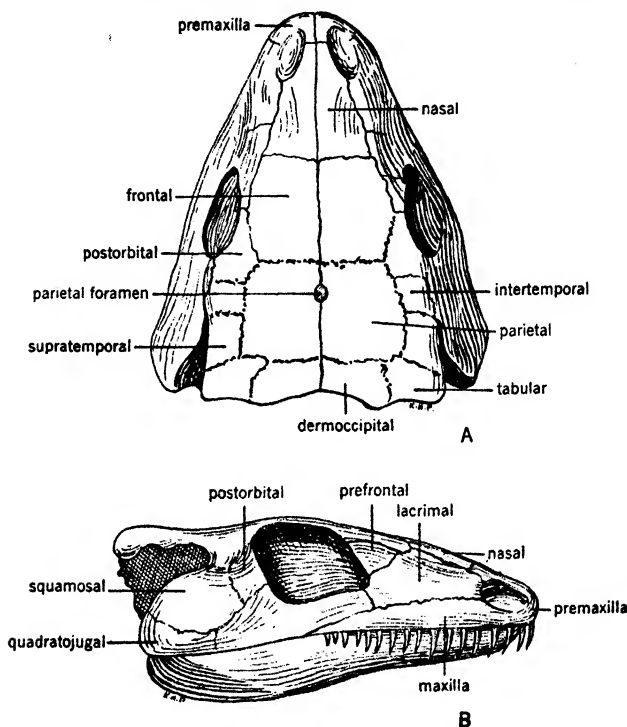


FIG. 102. Skull of a fossil amphibian, *Seymouria*. A, dorsal; B, lateral.

besides those for the sense organs, and ending with the lizards and *Sphenodon*, in which there are numerous fenestrations (Fig. 103).

Anapsidan Skull

The typical anapsidan skull (Fig. 103) without any openings or vacuities on the roof, is found in primitive reptiles known as cotylosaurs. In the earliest forms of cotylosaurs, the skull roof is not fenestrated but is similar to that of the reptile-like amphibian, *Seymouria baylorensis* (Fig. 102). The roofing bones consist of dermoccipitals, parietals, frontals, and nasals with a parietal foramen between the parietals. Laterally the roofing is filled in by the epiotics (tabular), supratemporals, intertemporals, postfrontals, prefrontals, and lacrimals. The sides of the skull are completed by the squamosals, quadratojugals, jugals, maxillae, and premaxillae. A notch permits the stapes to reach the tympanic membrane.

Synapsidan Skull

The Synapsida are ancient forms with no modern representatives except possibly the turtles. The skull of the mammals is probably derived from this type. The condition of the skull has been changed by the opening of a fenestra on the side of the skull, between the postorbital, squamosal and jugal (Fig. 103). The fenestra varies from a small slit to a large fossa. Among the Therapsida (Fig. 108), mammal-like reptiles, there is a close approach to the mammalian type of skull with heterodont dentition and two condyles. The reduc-

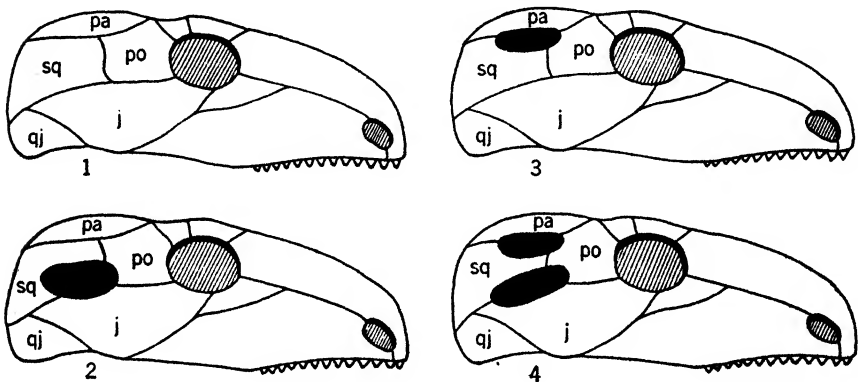


FIG. 103. Diagram showing the relation of the temporal arches in the reptiles. Examples: (1) anapsidan, *Cotylosaurs*; (2) synapsidan, *Cynognathus*; (3) parapsidan, *Araucoscelis*; (4) diapsidan, *Sphenodon*.

Abbreviations: pa, parietal; sq, squamosal; po, postorbital; j, jugal; qj, quadratojugal.

tion of the bones of the jaw region is suggested by the conditions found in such forms as *Ictodopsis* (Fig. 108), where the dentaries were greatly enlarged and had a process approaching the squamosal to form a new contact and a new mandibular condyle. The posterior mandibular elements were becoming reduced in size. The jugal and squamosal formed an arch, the teeth were in sockets, a secondary palate was being formed, there was a long external auditory meatus, and the quadrate was becoming quite small.

Skull of the Chelonians

The skull of the chelonian (Fig. 104) is very interesting because of the different conditions present in this one division of reptiles. Romer (1945) claims that the roof of the turtle skull may be emarginated and often incomplete, but it has never developed true temporal openings, and consequently he places the Chelonian in the Anapsida.

Species such as the primitive Triassic *Triassochelys* and *Chelone*, a modern sea form, appear to have the typical anapsidan condition with the skull roof resembling that of the cotylosaurs, yet, if the condition is to be considered primitive, several significant facts need

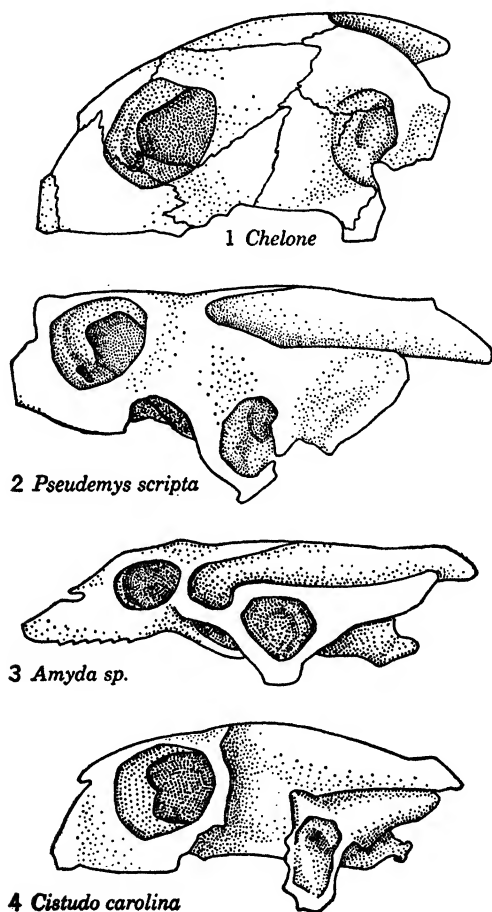


FIG. 104. To show the different conditions of the skull roof in a series of turtles. (1) Roof completely covered, with the exception of an incision at the posterior end of the skull roof. (2) Incision carried forward towards the eye region. (3) Incision continued leaving a narrow bar joining the eye and ear region. (4) Bar connecting eye and ear region obliterated entirely.

to be explained. No parietal foramen is present in these animals, and a number of bones, typical in the cotylosaur skull, are lacking. For this reason many anatomists assume that the roof is secondary structure and not primitive. Within the Chelonia, a series can be arranged showing all the stages from the complete roof of *Triassoschelys* and

Chelone to the terrestrial land turtles, such as *Terepene*, where the character of the skull shows a type fairly close to the synapsid condition. In *Terepene* the otic region is on the dorsal side of the skull; a very slight postorbital bar is posterior to the eye; and there is a lack of connection between the maxilla and the region of the quadrate. Because of the reasons stated above, the Chelonina may be included with the Synapsida (Fig. 103).

Forms other than sea-turtles show a specialization of the bones around the quadrate region by which a resonance chamber is developed.

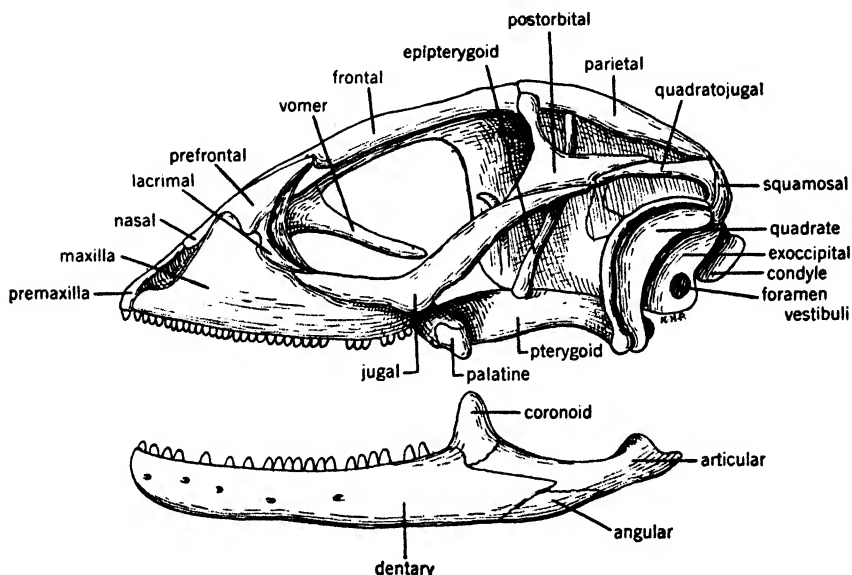


FIG. 105. Skull of *Sceloporus*, lateral aspect.

In *Amyda*, the squamosal is hollowed out to form a thin-walled chamber in connection with the tympanum. The stapes is able to reach the tympanum through a notch in the quadrate.

Diapsidan Skull

The Rhynchocephalia, of which *Sphenodon* (Fig. 103) is the only living representative, is most striking in its skull architecture, since it has two temporal arcades and a posttemporal fossa. There are numerous representatives of this diapsid type among the ancient reptiles. Crocodilia have a diapsid type of skull.

Parapsidan Skull

The lizards and snakes are modern representatives of the Lepidosauria. The skull of the lacertilians (Fig. 105) is usually very light

and of the streptostylic type, with a movable quadrate. The bones are not strongly articulated, and some of them are capable of slight movement. The Squamata, including the snakes and lizards, have only one temporal arch formed by the jugal and the squamosal, and even that is not always complete. They generally have a posttemporal arcade. This condition of the reptilian skull has been called parapsid. Romer (1945) maintains that the parapsid skull (Fig. 103) is derived from the diapsid type by the loss of the temporal bar.

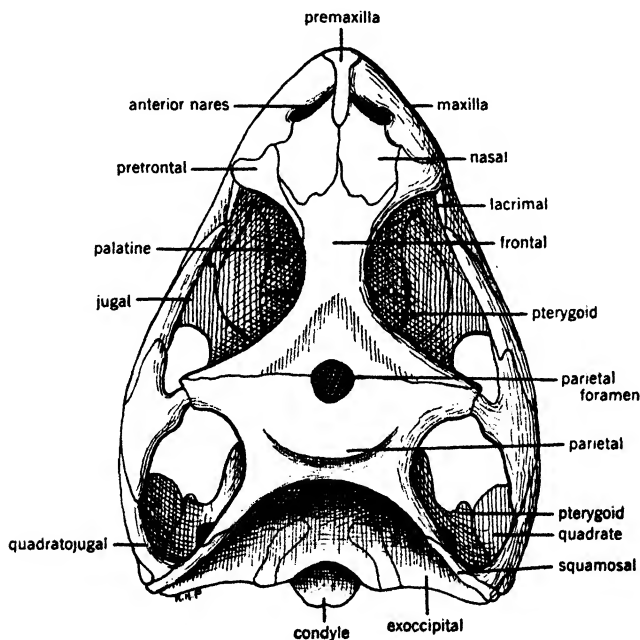


FIG. 106. Skull of *Sceloporus*, dorsal aspect.

The skull of *Sceloporus* (Figs. 105, 106) has a diapsid condition and illustrates the general characteristics of the reptilian skull. It differs in appearance from that of an amphibian, since it is not of the flat, platybasic pattern, but is the tropibasic type, characteristic of reptiles, in which there is more depth between the eyes, with some consolidation and simplification of the parts of the skull. The fish and modern amphibian skull differ radically, but the difference between *Sceloporus* and a modern amphibian is not nearly so striking. The paired condyles of the amphibians have been modified to one in the reptiles. The brain case is enlarged and is better protected, although the anterior end remains open. The four occipital bones are ossified, surrounding the foramen magnum. The dorsal side of the skull has a fenestra, or arcade, between the quadrate and the bones of the brain case. The

skull is narrow between the eyes, which are separated by a thin septum. The quadrate is not fixed but slightly movable, and hence of the streptostylic type as opposed to the monimostylic type in which the quadrate is fixed. The squamosal ties the quadrate to the skull dorsally, and a loose pterygoid connection on the ventral side supplies a brace in this region. In the monimostylic *Chelonia*, the quadrate is fixed solidly at all points. The ventral side of the skull shows a number of striking differences, since the parasphenoid, the large covering plate of the amphibian palate, is either lacking or a mere vestige. The posterior choanae open far back in the mouth, much farther than in the amphib-

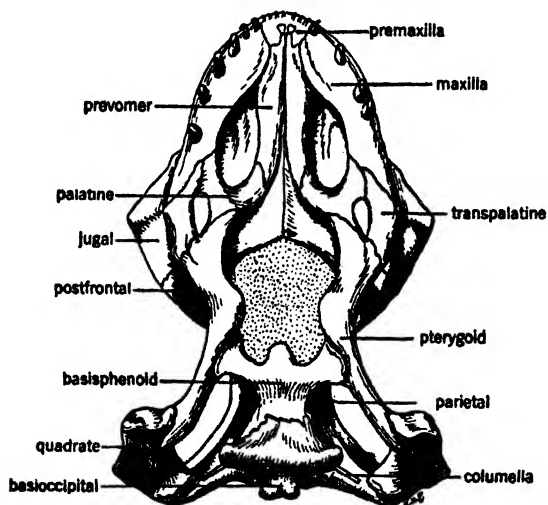


FIG. 107. Skull of *Heloderma*. Ventral.

ians. There is a large interpterygoid cavity, and the pterygo-palatine series is attached to the posterior end of the maxilla by a new element, the transpalatine, or ectopterygoid. The eipterygoid, or columella cranii, a bone peculiar to reptiles, is found in the lacertilians and in some other orders, forming a brace between the pterygoid and the parietal.

Reptiles may have teeth on the palatines, pterygoids, and other bones, but in *Sceloporus* they are found only on the dentary, premaxilla, and maxilla. The teeth in *Sceloporus* are pleurodont (Fig. 76), that is, firmly fixed to the sides of the jaw. The dentary has twenty-eight teeth, the premaxilla eight, and the maxilla about twenty-four. The teeth are long, open at the root end, and held to the inside of the jaw by connective tissue.

In the lizard *Heloderma* (Fig. 107), the skull is roofed over by the parietals, frontals, post- and prefrontals, nasals, and lacrimals. The

lateral series of the roof are the premaxilla, maxilla, jugal, and the squamosal and quadrate. The base of the skull is typically lacertilian, the median series consisting of the basioccipital, basisphenoid, a cartilaginous parasphenoid, pterygoid, transpalatine, epipterygoid, palatines, and prevomer. The condyle is formed by the basioccipital for the most part, since the exoccipitals enter but slightly into its structure. The otic series, all being joined with the exoccipitals and other bones of the region, are not evident as separate elements. The long thin stapes extends to the tympanum, which is stretched in the otic notch of the quadrate. The gap between the brain case and the anterior part of the skull is filled by a cartilaginous wall representing the unossified pleurospenoids (alisphenoids).

In the snakes the skull is more specialized than in the lizards and its streptostylism is more pronounced, since all the elements except those of the brain case are movable. The articulations are of the loose,



FIG. 108. Skull of *Ictidopsis*, a mammal-like reptile.

contact type so that the greatest freedom of movement is obtained. The quadrate extends posteriorly and is joined to the skull by the squamosal. The jugals and epipterygoids have been lost, and the orbito- and pleurospenoids (alisphenoids) usually ossify. The bones of the mid-dorsal line are the supraoccipital, parietals, frontals, nasals, and premaxillae. The brain case is formed by the ventral extensions of the frontals and parietals, which form the dorsal walls and a part of the sides, with the prootics, exoccipitals, basioccipital, and basisphenoid completing the structure. The squamosal is not included in the brain case. The premaxillae, maxillae, palatines, transpalatines, pterygoids, and dentaries have teeth. The stapes extends from the fenestra vestibuli to the quadrate, since no tympanum is present. The pterygoid, attached to the movable quadrate, forms a part of the series consisting of the pterygoids, transpalatines, palatines, and maxillae. All these permit a maximum of movement and the independent use of the two sides, the series acting as levers to pull the food down into the throat. They are assisted by the two mandibles working separately with an antero-posterior movement. By means of their highly modified jaw

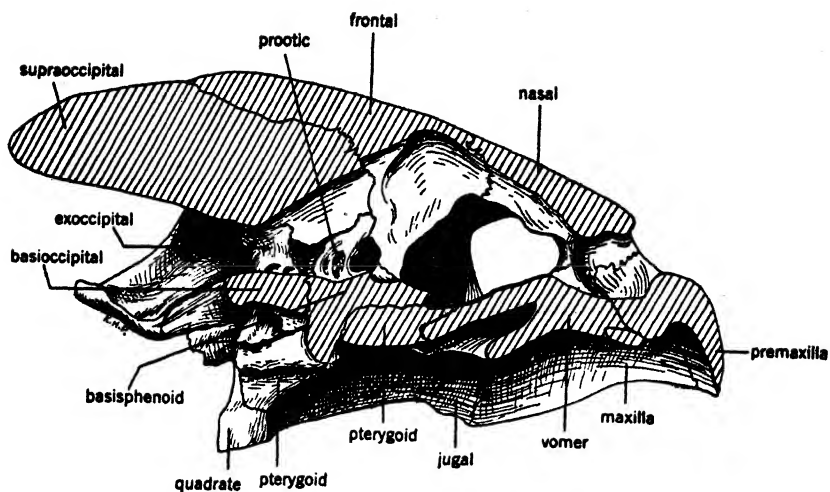


FIG. 109. Skull of sea-turtle (*Thalassochelys caretta*). Sagittal section.

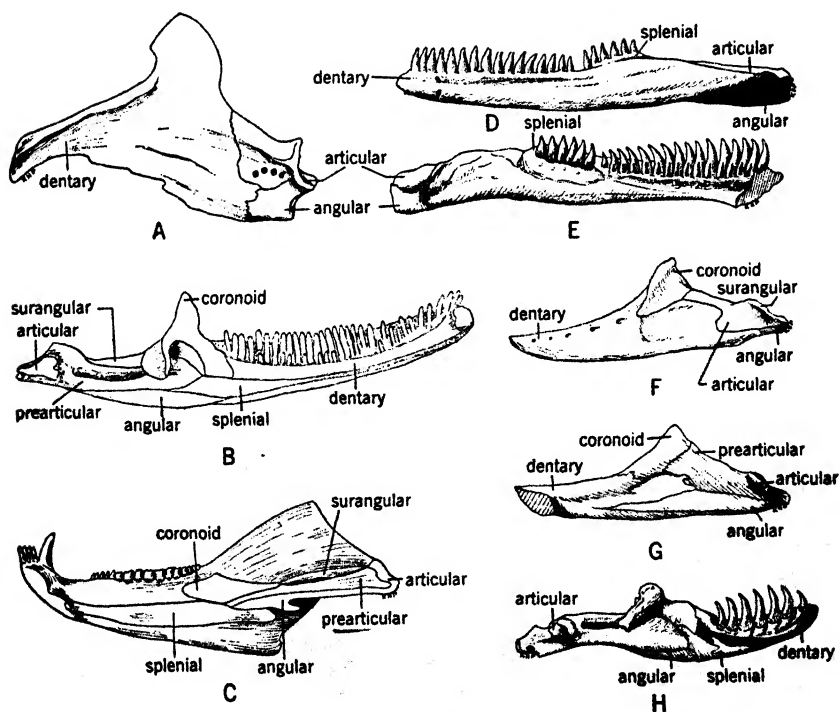


FIG. 110. Mandibles of different vertebrates to show their structure and elements. A, left mandible of carp (*Cyprinus carpio*); B, mandible of *Sceloporus undulatus*, inner face of left; C, inner face of mandible of cynodont lizard (after Broom); D, outer face of left mandible of *Necturus*; E, inner face of mandible of *Necturus*; F, outer face, and G, inner face, of mandible of turtle (*Amyda spinifera*); H, mandible of *Heloderma*, left, inner face.

apparatus, snakes are able to swallow animals much larger in diameter than themselves.

Reptilian Jaw

The jaw elements of the reptiles are generally more numerous than in modern amphibians. In the lizard *Sceloporus*, the mandible (Fig. 105) consists of seven bones: a dentary, coronoid, articular, angular, surangular, goniale, and splenial. Meckel's cartilage is reduced to a slight cartilaginous rod in a groove at the posterior end of the jaw and continuous with the articular. The articular forms the surface for articulation with the skull. *Heloderma* (Fig. 110) has a dentary,

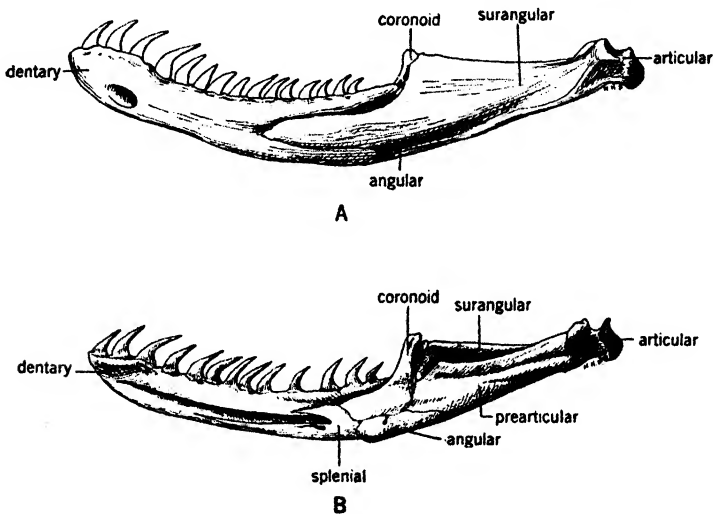


FIG. 111. Mandible of python. A, outer; B, inner face.

splenial, angular, surangular, and coronoid. Crocodiles and alligators have the same bones in their jaw. The union at the symphysis is variable, snakes (Fig. 111) generally retaining a loose symphysis, whereas in other reptiles it is ankylosed.

The therapsid jaw is quite significant, since it is used to explain the origin of the ossicles of the ear in mammals. The dentary is large, but the posterior elements are greatly reduced in size. There is an indication of a new articulation between the posterior end of the dentary and the squamosal.

Avian Skull

The skull of birds is very light and pneumatic, resembling that of pterodactyls, in some respects, with a tendency for all the individual

elements to fuse into one piece, except the quadrates, which remain free and movable (Fig. 112). Teeth, the absence of which separates the birds from the modern reptiles, were present in *Archaeopteryx*, *Hesperornis*, and *Ichthyornis*. Modern birds have the jaws encased in a horny beak, resembling that of the turtles.

The skull is tropibasic and, since the quadrate is free, is streptostylic. The brain case is large, a feature that also separates the birds from the reptiles. The foramen magnum is inclined ventrally, and in owls and hawks its position is clearly ventral. The occipital condyle is formed

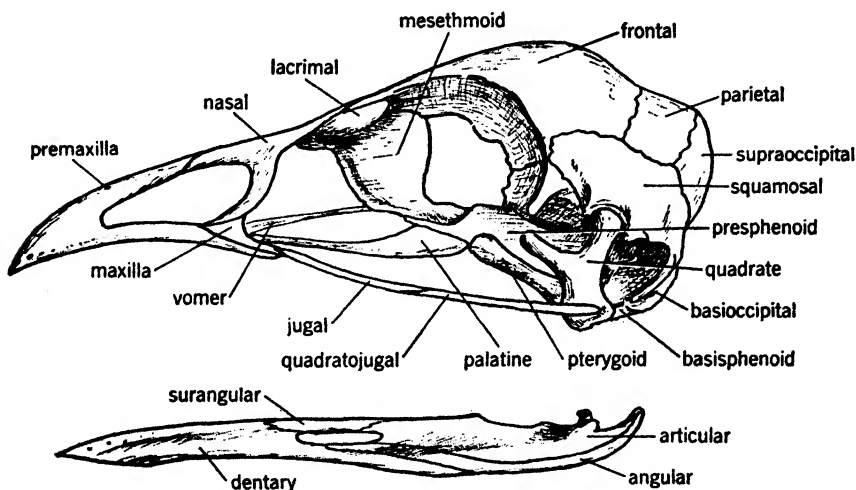


FIG. 112. Skull of chicken.

by the basioccipital. There is much variation in the base of the skull and in the formation of the palate—so much that it has been used in separating the different groups of birds. The skull is fused in the adult so that the separate bones are not distinguishable, and young forms must be studied to separate the skull elements.

The separate bones of the skull (Fig. 112) fuse early, and most of the sutures are obliterated in the adult. The brain case, which is particularly well knit together, is formed by the fusing of the frontals, parietals, four occipitals, orbito- and pleurosphenoid, squamosal, basisphenoid, the bones of the otic capsule, and a vestigial parasphenoid. Three series of bones extend forward from the brain base: (1) the nasal, ethmoid, and premaxilla constitute a dorsal series extending forward from the frontal; (2) the quadrato-jugal, jugal, and maxilla form a lateral series extending from the quadrate to the premaxilla; (3) a ventral median series, consisting of the pterygoid and palatine, connect the quadrate with the premaxilla. The chicken has a large bony sep-

tum, the interorbital, which may be called the median ethmoid. Because of the loose quadrate, some movement is possible in the maxilla and premaxilla. A conspicuous lacrimal with a long ventral spine is in the usual position in the anterior corner of the eye socket. The orbits are comparatively large. The mandible is quite reptilian in its character, usually consisting of a dentary, splenial, surangular, articular, coronoid, and dorsal coronoid, all of which may be quite fused together in the adult. (See Fig. 112.)

Mammalian Skull

In mammals the skull differs from that of other vertebrates by having a larger brain case, double condyles, heterodont dentition, with teeth

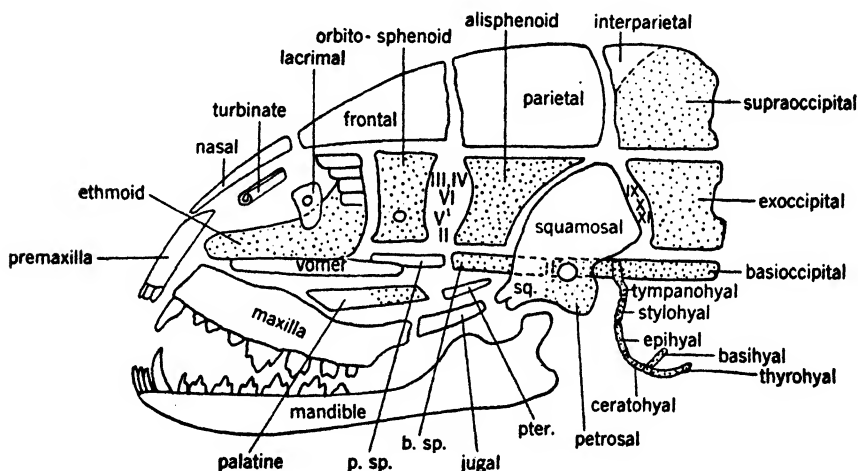


FIG. 113. Diagram of mammalian skull, cartilage bones stippled, dermal bones white. Redrawn from Weber.

only on the premaxillae, maxillae, and mandibles (Fig. 113). Reptilian bones not appearing in mammals are the prefrontals, postfrontals, transpalatines, supraorbitals, and quadratojugals. The alisphenoid is not homologous with the bone of the same name in reptiles but is probably derived from their epipterygoid. The transpalatine (ectopterygoid) of reptiles may possibly appear in the pterygoid process of mammals, formed by the fusion of the transpalatine with the endopterygoid. The vomer of mammals appears to have been derived from the parasphenoid of the lower vertebrates and, consequently, is not homologous with the bone of the same name in the other classes. The posttemporal fossa is not present in mammals except in the monotremes. The two occipital condyles are formed from the exoccipitals, as in amphibians. The various sphenoid bones tend to combine and form

one element. The prootic, epiotic, and possibly the opisthotic fuse in mammals to form the petrosal bone, which encloses the inner ear. The petrosal, in turn, fuses with the squamosal and other elements to form the complex temporal bone of mammals. The squamosal forms the new articulation for the mandible. There are three ear ossicles (Figs. 87, 349): the stapes, derived from the hyomandibular; the incus, derived from the quadrate; and the malleus, generally thought to be the articular. The tympanic bone appears to have been derived from the angular of the reptiles. Many mammals develop a tympanic bulla,

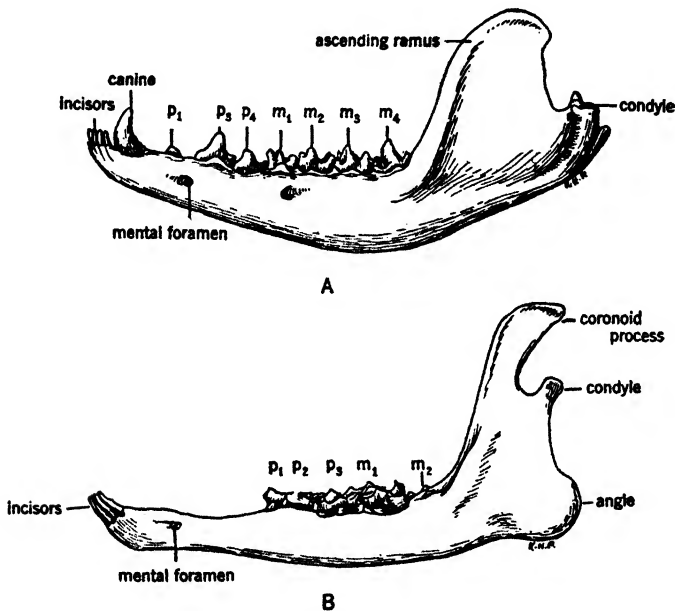


FIG. 114. Mammalian mandibles. A, opossum; B, deer.

a thin-walled, blister-like structure forming a resonance chamber to the middle ear (Fig. 121, auditory bulla). The mandible consists of a pair of bones, the dentaries, which fuse at the symphysis in some adults.

The importance of a number of reptilian elements is lessened considerably in the mammalian skull because of the new architecture and the great enlargement of the brain case. The brain case is now completely enclosed, the ethmoid forming a cribriform plate at the anterior end for nerve twigs from the olfactory tract (Fig. 120). The occipitals usually ankylose into one piece, forming the posterior wall; the parietals, temporals, and frontals form the roof and most of the sides; the rest is filled out by the orbito- and alisphenoids (epiterygoid) (Figs. 87, 118). The floor is formed by the occipital, basisphenoid, presphen-

oid, and temporal, together with the two lateral bones, the orbito- and alisphenoid (Fig. 115). The greatest change in the basicranial region comes because of the shift of the quadrate into the ear. The quadrate in other groups has been the center for the articulation of elements connected with the palate; and with its loss, this series loses its importance. The temporal depends on its articulation with the brain case for its bracing, which makes it secure and removes the need for outside supports. The jugal (malar or zygomatic) is extremely important as a brace for the maxillae, especially in forms with great stress

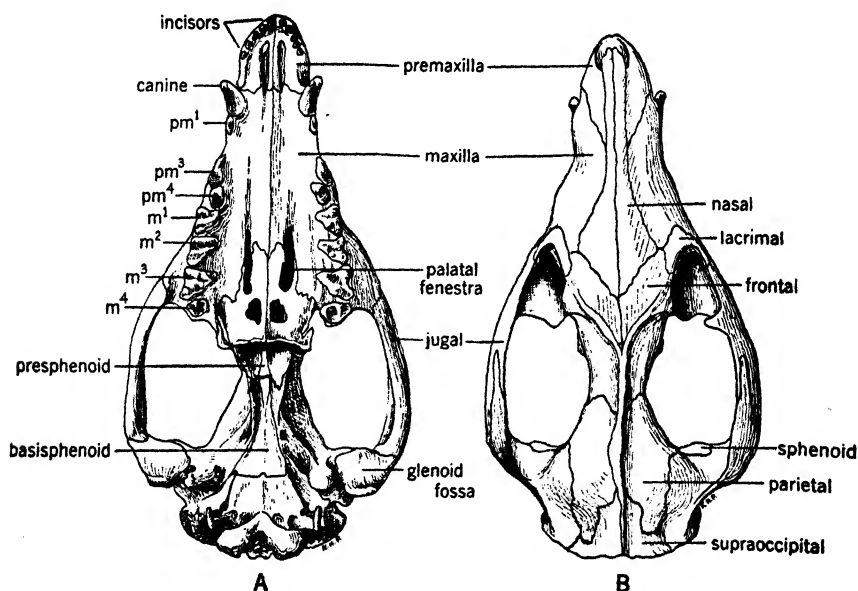


FIG. 115. Skull of opossum (*Didelphis*). A, ventral; B, dorsal.

on the molars, as in carnivores. The pterygoids and palatines no longer serve as braces and become minor elements. The palatines together with the maxillae form a secondary shelf, the hard palate, ventral to the old mouth roof. This new palate (Figs. 116, 117 B, 121) is suggested in the alligators, where the internal nares are far back because of the mesial growth of the maxillae.

Although the skulls of all mammals show a general similarity, some striking differences separate the monotremes, marsupials, and placental mammals. The monotremes retain a number of reptilian characters not found in the more advanced mammals, such as a posttemporal arcade and a prevomer, or dumbbell bone. The palatines and pterygoids enter into the formation of the brain case, a condition not found in the higher mammalian groups. The marsupials have a fenestrated

palate (Fig. 115 A), an inflected angle on the mandibles, and a brain case of comparatively small size. The dentition (Fig. 115 A) of the

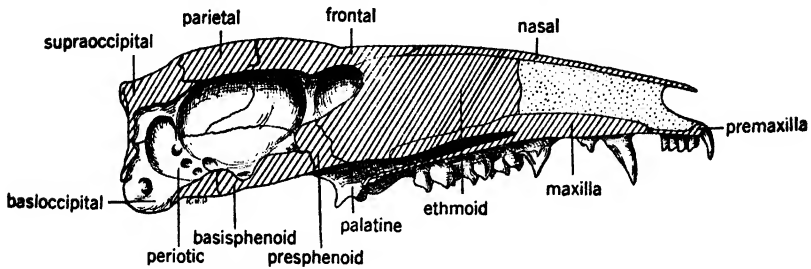


FIG. 116. Sagittal section through skull of opossum (*Didelphis*).

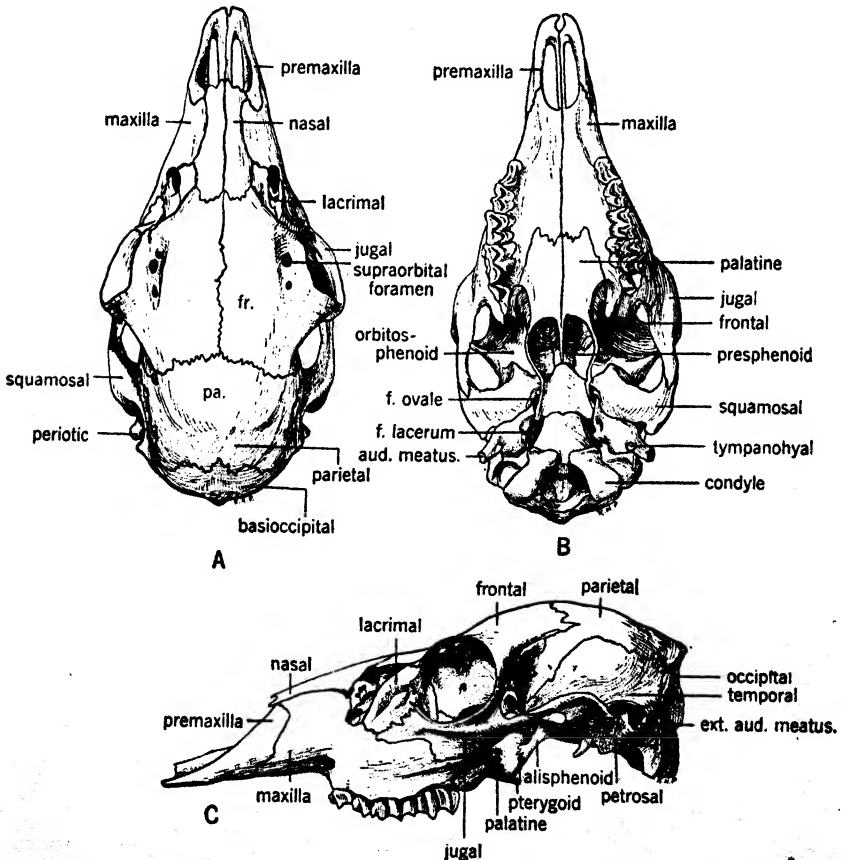


FIG. 117. Skull of mule deer (*Odocoileus*). A, dorsal; B, ventral; C, lateral.

marsupials is sufficient to distinguish them from the placentals. In placental mammals, the brain case is greatly enlarged, the characters of

the marsupials are lacking, and the dentition is very different. The brain case becomes progressively larger in the placentals (Figs. 117 C, 118), with a corresponding reduction in the size of the facial elements, until in the primates the brain case makes up most of the skull and extends over most of the facial elements.

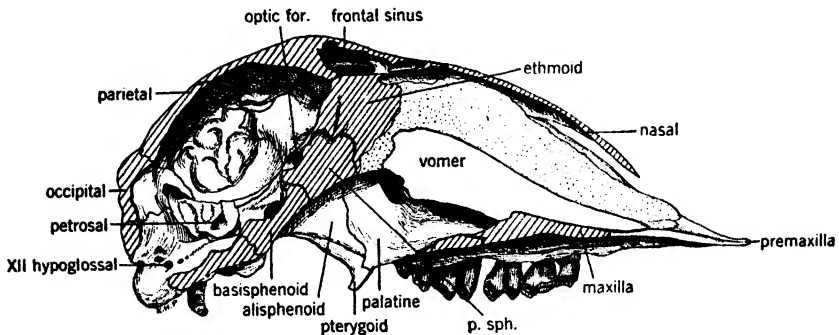


FIG. 118. Skull of domestic sheep, sagittal section.

Foramina

The roof of the mammalian skull (Figs. 115 A, 117 A) is left fairly intact with only a few small openings for minute nerves and blood vessels, but the sides and the floor are pierced by numerous openings, through which the cranial nerves and blood vessels may either enter or escape from the skull. Although a number of foramina and openings are formed on the lateral side, it is on the ventral face that most of them appear (Figs. 119, 120, 121, 122).

Cranial foramina are for the most part surprisingly uniform in the class Mammalia. A few are variable and may be confluent with some other foramen or missing entirely. They are very useful in classification, since the presence or absence of certain foramina differentiates orders very clearly. The general position of the foramina is practically fixed early in the history of the tetrapods, and subsequent changes are related to changes in the structures that extend through the skull or in the skull itself. The foramina and openings of the skull are of course fixed at an early period of embryological development, so that the vessels and nerves establish their position before the bones and definite outline materials are formed. The vessels and nerves appear first, and the bones either form around them or the vessels are left between sutures. There are numerous small foramina that are not stable, but subject to much variation both in position and size, that transmit small nerves or blood vessels. The parietal foramen present in some mammals is not common in the dog and the cat.

FORAMINA OF THE DOG SKULL

Foramen	Bones concerned	Structure transmitted
1. Infraorbital canal	Maxilla	V ² branch of V
2. Lacrimal	Lacrimal bone	Naso-lacrimal duct
3. Sphenopalatine	Palatine	Sphenopalatine nerve and artery
4. Posterior palatine	Palatine	Palatine nerve and artery
5. Ethmoid	Frontal	Ethmoid branch of V ¹
6. Optic	Orbitosphenoid	Optic tract
7. Sphenoidal (Orbital fissure)	Between orbito-, ali- and basisphenoid	Nerves III, IV, V ¹ , VI
8. Anterior pterygoid	Ali- and basisphenoid	Maxillary branch or V ²
8 ^a . Rotundum	Basisphenoid	Maxillary branch or V ² outlet of external carotid
9. Posterior pterygoid	Alisphenoid	External carotid
10. Ovale	Alisphenoid	V ³ of trigeminus
11. Posterior glenoid	Squamous portion of temporal	Vein from the transverse sinus of meninges
12. External auditory meatus	Bulla of temporal	Inlet to tympanum of ear
12 ^a . Internal auditory meatus	Petrous portion of temporal	Nerves VII and VIII
13. Eustachian	Between bulla and alisphenoid	Tuba auditiva
14. Carotid	Through temporal ventral to bulla	Loop of the internal carotid extends into this foramen
15. Stylomastoid	Between temporal and basioccipital	Exit of VII
16. Incisive	Between maxilla and premaxilla	Connects with Jacobson's organ, transmits nasopalatine nerve. Stenson's duct, and palatine nerve
17. Anterior palatine	Between maxilla and palatine	Palatine nerve
18. Jugular	Between bulla and basioccipital	Nerves IX, X, XI, internal carotid, veins from the meningeal sinus
19. Hypoglossal	Occipital bone	Nerve XII
20. Foramen magnum	Occipital bone	Spinal cord, veins and arteries from brain case
21. Condylar canal	Occipital bone	Condylar vein from meninges
22. Mandibular	Mandible	V ³ and blood vessels
23. Mental	Mandible	Branch of V ³ to chin and blood vessels

Skull Foramina

1. *Infraorbital*. This foramen is constant in mammals, but is quite variable in shape and size. It is large in some rodents, for a

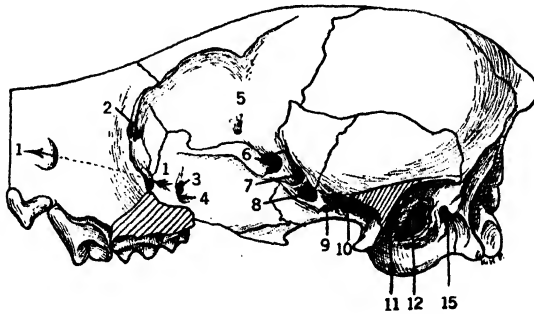


FIG. 119. Skull of dog showing lateral foramina. (See table of foramina.)

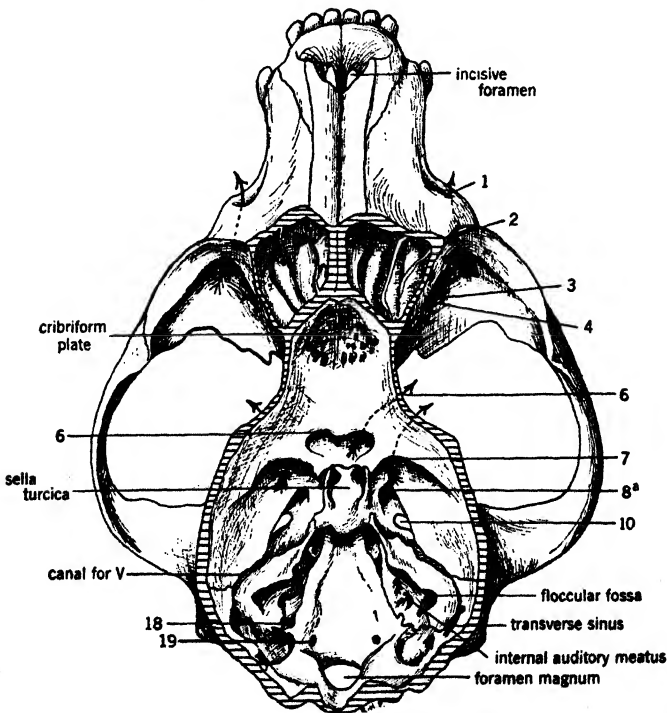


FIG. 120. Skull of dog with cranial roof removed to show foramina. (See table of foramina.)

part of the origin of the masseter muscle extends into its cavity. It transmits the maxillary branch of the trigeminus nerve (V^2) and some blood vessels. (Figs. 119, 120.)

2. *Lacrimal*. The lacrimal bone is usually pierced by the nasolacrimal duct which connects the corner of the eye with the nasal cavity. It is lacking in pinnepeds and a few other orders. (Figs. 119, 120.)

3. *Sphenopalatine*. The foramen is on the lateral face of the palatine bone, and is the more dorsal of two small openings in this region. It transmits the sphenopalatine nerve, a branch of V^2 , and an artery to the nasal cavity. (Figs. 119, 120.)

4. *Posterior Palatine*. The foramen is ventral to the sphenopalatine and extends through to the anterior palatine foramen which is its outlet to the palate (foramen 17). It transmits the palatine nerve (a twig from V^2) and a small artery. (Figs. 119, 120.)

5. *Ethmoid*. A small foramen on the side of the orbit, on the fronto-sphenoid suture. Transmits a branch of the palatine nerve, a twig of V^1 , and is fairly constant in mammals. (Figs. 119, 120.)

6. *Optic*. A constant foramen in mammals, that usually pierces the orbitosphenoid bone, although originally it probably came through the foramen lacerum anterior. It transmits the optic tract. (Figs. 119, 120, 121, 122.)

7. *Sphenoidal*. The sphenoidal is the second of the three main foramina which, in the dog, either pierces the orbitosphenoid or is formed along its lateral border. Its position is really between the orbitosphenoid and the alisphenoid. In some animals it is confluent with the optic foramen (marsupials). It transmits nerves oculomotor, trochlear, a branch of the trigeminus (V^1), abducens, and may carry an additional branch of the trigeminus (V^2). This is often called the orbital fissure. (Figs. 119, 120, 121, 122.)

8. *Anterior Pterygoid*. This foramen pierces the alisphenoid bone and is the third, in the row along the sides of the alisphenoid and orbitosphenoid, in the dog skull. It is confluent with the opening of the foramen rotundum (8^a), so that it is not clearly visible from the outside of the skull, since the flange of bone that forms the carotid canal somewhat covers it. The external carotid of the dog is enclosed in bone, and the anterior pterygoid is its outlet. This canal, known as the alar or alisphenoid canal, is present in many mammals, but lacking in monotremes, marsupials, artiodactyls, and others. (Figs. 119, 120, 121, 122.)

8^a. *Foramen Rotundum*. This foramen pierces the sphenoid bone between the basisphenoid and the alisphenoid, and transmits a branch of V^2 . (Fig. 122.)

9. *Posterior Pterygoid*. The foramen is confluent with the opening of the foramen ovale (the pterygoid canal, taken up under 8, is the canal formed by a flange from the alisphenoid bone that extends dorsally, forming a canal for the external carotid). (Figs. 119, 121.)

10. *Foramen Ovale*. This foramen, which is lateral to the glenoid fossa in the dog, is large and distinct. The entrance to the carotid canal is just mesial to it. Ovale transmits the mandibular branch of the

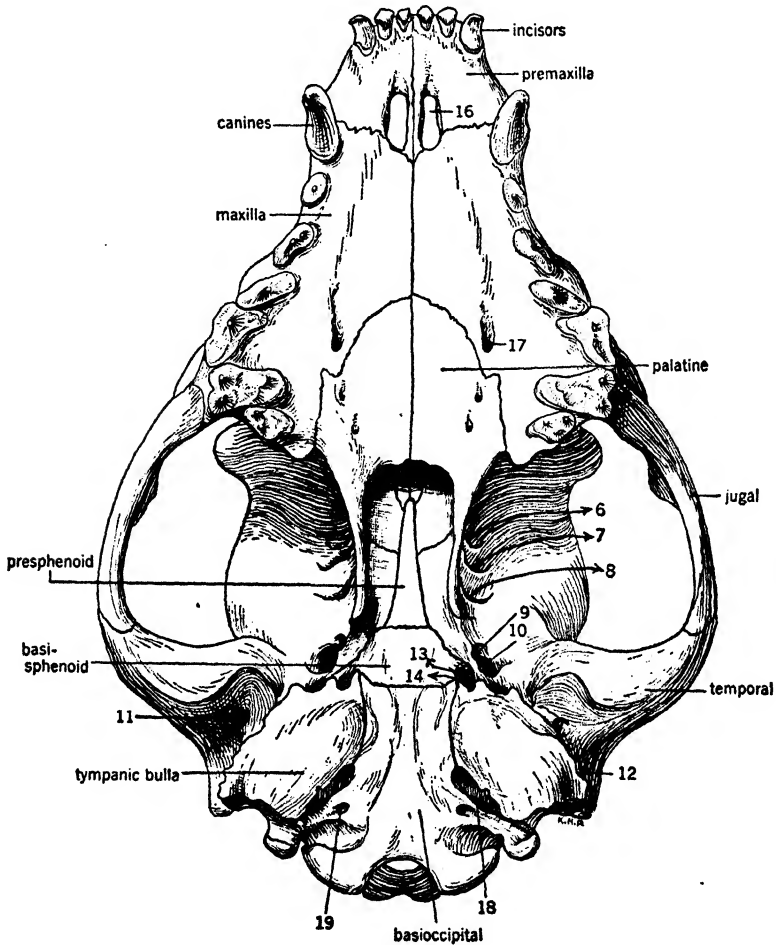


FIG. 121. Ventral view of dog skull showing foramina. (Numbers correspond to names in the table of foramina, p. 173.)

trigeminus (V^3), and is in a position so that the nerve can easily descend and reach the mandibular foramen on the inner side of the jaw. (Figs. 119, 121.)

11. *Posterior Glenoid*. Lateral to the bulla and posterior to the prominent glenoid process, this foramen is large and well differentiated in the dog. It transmits a vein from the transverse sinus to the brain case. (Figs. 119, 121.)

12. *External Auditory Meatus*. This large opening on the lateral side of the bulla leads to the tympanic membrane of the ear. The opening is prominent in mammals with an inflated bulla, but may be at the end of a bony tube in animals having a heavy, flat bulla. (Fig. 119; Fig. 117.)

12^a. *Internal Auditory Meatus*. At about the middle point of the mesial face of the petrosal bone, a deep foramen transmits the auditory (VIII) and the facialis (VII). (Fig. 122.)

13. *Eustachian (Tuba Auditiva)*. The antero-mesial wall of the tympanic bulla ends in a rough, serrated edge, through which two openings appear in the dog. The more lateral of the two openings, with rough edges, is the Eustachian, through which extends the tuba auditiva or Eustachian tube. The more mesial opening is the carotid foramen. (Fig. 121.)

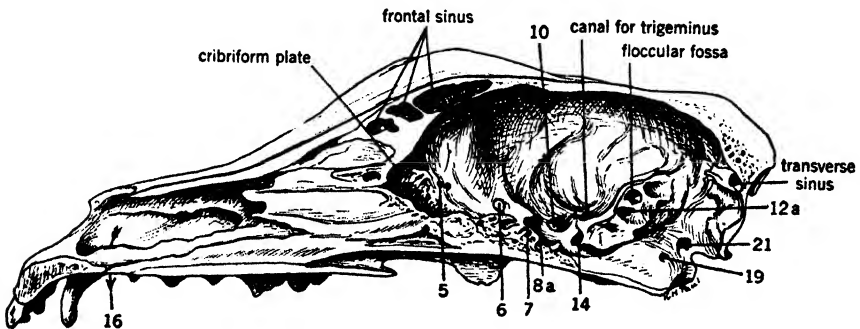


FIG. 122. Sagittal section of dog skull, showing foramina.

14. *Carotid Foramen*. This is mesial to the Eustachian tube opening, and is anterior to the auditory bulla. Its outline is smooth compared to the opening of the Eustachian tube. A loop of the internal carotid extends down into this foramen, but does not go through, since the loop returns to the skull cavity, immediately after making the loop, to supply the meninges and the brain. (Figs. 121, 122.)

15. *Stylomastoid*. This is a small foramen at the posterior-mesial edge of the bulla, anterior to the large ventral process of the basioccipital. It transmits the facial nerve (VII) to the outside of the skull. (Fig. 119.)

16. *Incisive* (anterior palatine of some authors). These foramina are large and distinct in the dog, their borders being formed by the premaxilla and maxilla. In some animals they are almost confluent. They transmit the naso-palatine nerve (a branch of V²), Stenson's duct, and connect with Jacobson's organ. (Figs. 120, 121, 122.)

17. *Anterior Palatine*. This foramen is on the roof of the mouth,

lateral to the midline, and lies between the maxilla and the palatine. (There are often one or more other small foramina in this region, but they are small and irregular.) The foramen transmits an artery, which goes through to the floor of the nasal passage. (Fig. 121.)

18. *Jugular*. This foramen is the large, irregular opening, between the posterior face of the auditory bulla and the basioccipital. It transmits cranial nerves, glossopharyngeal, vagus, spinal accessory, and a large vein from the transverse sinus, and it is the entrance of the internal carotid to the brain case of the skull. (Figs. 121, 122.)

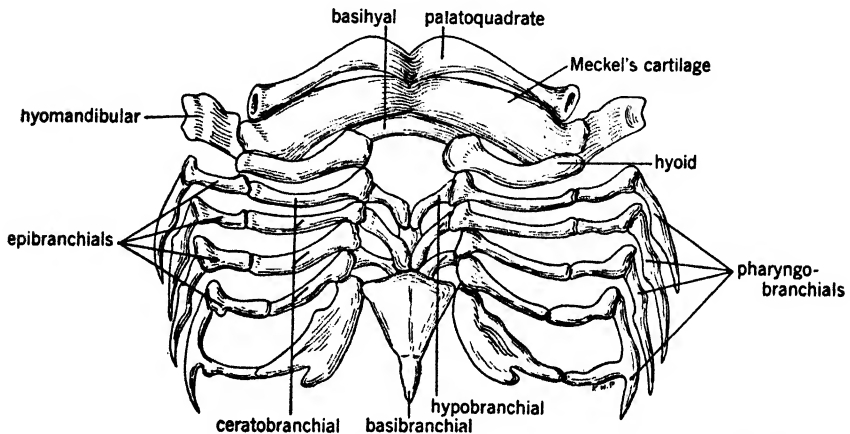


FIG. 123. Ventral aspect of visceral skeleton of a shark (*Squalus acanthias*). After Wells.

19. *Hypoglossal*. This nicely formed round foramen is just posterior to the jugular foramen (18). It pierces the basioccipital bone and transmits cranial nerve hypoglossal (XII). (Figs. 120, 121, 122.)

20. *Foramen Magnum*. This, the largest foramen of the skull, is surrounded by the occipital bone. It transmits the spinal cord, and arteries and veins connected with the brain case. (Fig. 120.)

21. *Condylar Canal*. This large foramen, in the lateral wall of the foramen magnum, transmits a large vein from the brain sinuses. (Fig. 120.)

22. *Mandibular Foramen*. This large foramen is on the inner side of the mandible, just anterior to the condyle. It transmits the mandibular branch of the trigeminus (V^s) and blood vessels to the teeth and the inner region of the mandible. A part of this nerve extends through the mandible and comes out again at the mental foramina to continue as the mental nerve.

23. *Mental Foramen*. This opening is on the lateral side of the mandible and usually ventral to the first or second premolar. Often

smaller foramina appear in this region of the jaw. The foramen transmits the mental nerve, a branch of V^3 , and blood vessels. (Fig. 114 B.)

Visceral Skeleton

The visceral skeleton consists of the skeletal structures originally supporting the gills and surrounding the pharynx. These structures

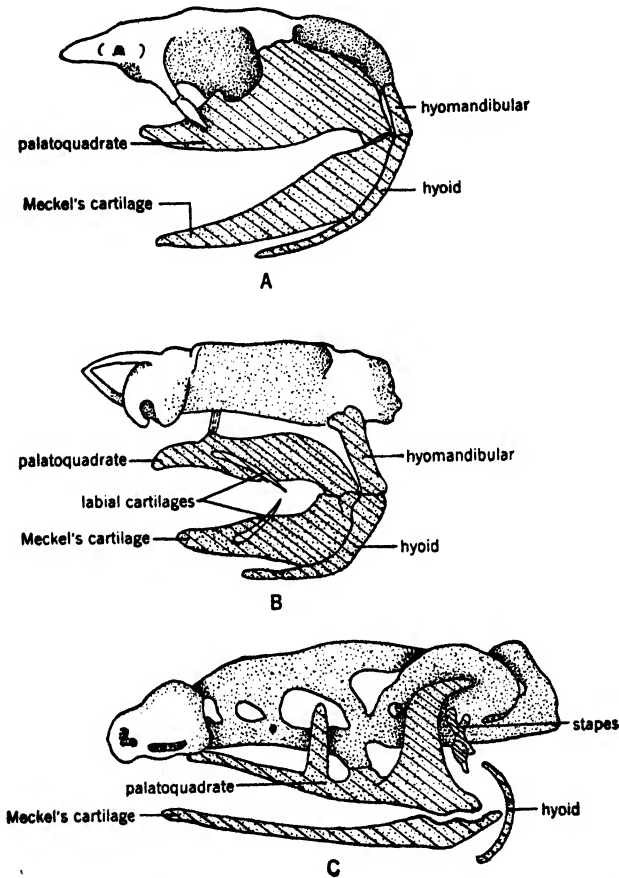


FIG. 124. Attachment of jaws to skull. A, amphistyle (primitive shark); B, hyostyle (*Squalus acanthias*); C, autostyle (chondrocranium of a tetrapod). After Goodrich.

consist typically of seven arches although their number may exceed this in earlier vertebrates. The first two arches contribute to the formation of the skull of higher vertebrates as already described. The other arches serve primarily as branchial arches to support the gills.

The first arch gives rise to the primitive jaws as seen in the Chondrichthyes (Fig. 85), where the arch has folded forming the palato-

quadrate cartilage for the upper jaw and the Meckel's cartilage for the lower jaw. Just posterior to the jaws, the second or hyoid arch divides into dorsal hyomandibular and ventral hyoid portions and tends to aid in the support of the jaws. In the most primitive sharks, the attachment is amphistylic (Fig. 124 A), both the mandibular and the hyoid arches being firmly attached to the skull.

The hyostylic attachment (Fig. 124 B), present in *Squalus*, is formed by both the mandibular and hyoid arches being attached to the chondrocranium by ligaments, the hyoid being functional in the support of the mandibular cartilages.

The autostylic (Fig. 124 C) attachment found in the higher forms has the palatoquadrate bar firmly attached to the skull, the hyoid arch taking no place in the suspension. The lower jaw and the palatoquadrate bar bear teeth in the sharks, and it is over this cartilaginous foundation that the dermal bones of the higher forms are to be deposited.

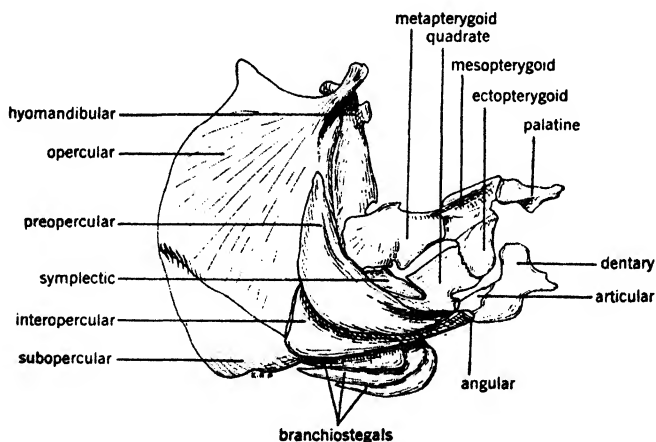


FIG. 125. Right opercular series, pterygoids and mandible of a carpsucker (*Carpiodes carpio*).

Visceral Arches of Fishes

The visceral skeleton is a development associated with gills and their external openings, the gill slits, which open and close in the work of respiration. The original reinforcing structure for the attachment of muscles was a series of bars or arches, varying in number from seven to nine, and possibly even more in ancient forms. In the sharks of the present day, each arch consists of several pieces of cartilage joined to a basal bar (Fig. 123). The dorsal piece, the pharyngo-branchial, is followed by an epi-, cerato-, and hypobranchial, with a basibranchial extending along the ventral bases. The labial cartilages

of the shark possibly represent extra gill cartilages. The jaws of the shark and their supports are derived from the two anterior gill arches, the first forming the mandibular arch and part of the second the hyomandibular; the remaining arches support the gills. In tetrapods, these arches are utilized for other purposes or eliminated. The visceral arches of *Amia* are slightly but not completely ossified, the mandibular and hyomandibular regions being covered with bony plates after the manner of the higher teleosts. In teleosts most of the parts of the visceral arches are ossified, and in some groups very interesting modifications are associated with food habits, as in the carp where the last pharyngeals bear peculiar tooth-like structures. The lower mandible

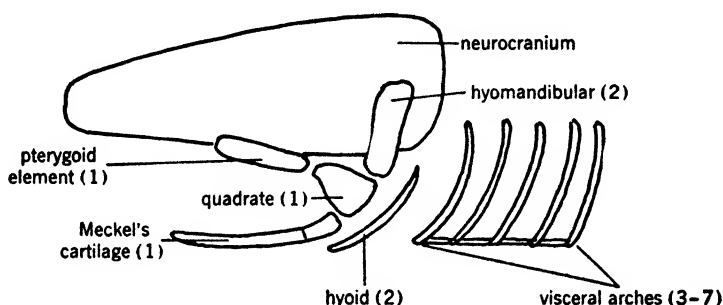


FIG. 126. Diagram showing relation of visceral elements to neurocranium in higher fishes.

of the teleosts, although sheathed with dermal bone, still retains Meckel's cartilage. The proximal end of Meckel's cartilage has ossified to form the articular which articulates freely on the quadrate of the pterygoquadrate portion of the first visceral arch (Fig. 126). The hyomandibular of the second arch serves to connect the quadrate with the neurocranium. The lower part of the second arch forms the hyoid (Fig. 127) which has been described on page 151. The remaining arches support the gill structures.

Visceral Arches of Amphibians

The visceral arches of the Amphibia (Fig. 128 A) are still somewhat fish-like, especially in the urodeles, but are more specialized in the Anura. The visceral skeleton of *Necturus*, exclusive of the jaws, consists of the hyoid series, involving part of the second arch, with remnants of four more arches, as indicated by three epibranchials and traces of a fourth. This structure in *Necturus* is associated with the permanent retention of gills. In *Rana catesbiana*, the visceral skeleton is an irregular piece, with parts much consolidated. The young tadpole

has four epibranchials but loses them during metamorphosis.

Noble has shown that, by means of endocrine gland extracts, certain changes can be initiated in forms that do not metamorphose normally, and that there is an attempt on the part of the visceral skeleton to approach the adult condition.

Visceral Arches of Reptiles

Reptiles retain a hyoid structure containing parts of the hyoid or second arch and may have remnants of the third and fourth visceral arch

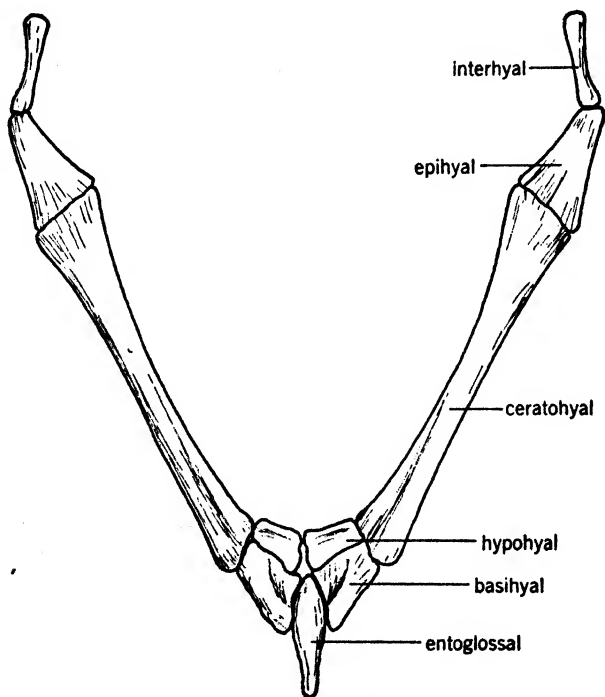


FIG. 127. Hyoid structure of codfish derived from second visceral arch.

arches. Parts of other visceral arches have probably contributed to the development of the laryngeal and tracheal cartilages which were but slightly developed in the amphibians.

The visceral skeleton of the *Chelonia* (Fig. 128 B) consists of a bony basal plate and two epibranchials. *Chelydra serpentina* has a narrow basilingual plate, and the hyoid or second arch is reduced to a pair of small cartilages extending out laterally. Posteriorly two pairs of cornua extend from the basal plate and represent the third and fourth visceral arches.

The visceral skeleton of the lacertilians (Fig. 128) consists of a number of parts of the old visceral structures of fishes. The anterior lingual process extends into the tongue, ending in cartilage. The median body is formed by the basihyoid, with two pairs of lateral elements, the anterior (hyoid) cornua and the posterior (branchial) cornua. The median basibranchials are shorter and cartilaginous. The visceral skeleton is well supplied with muscles and acts as a support for the glottis and the tongue.

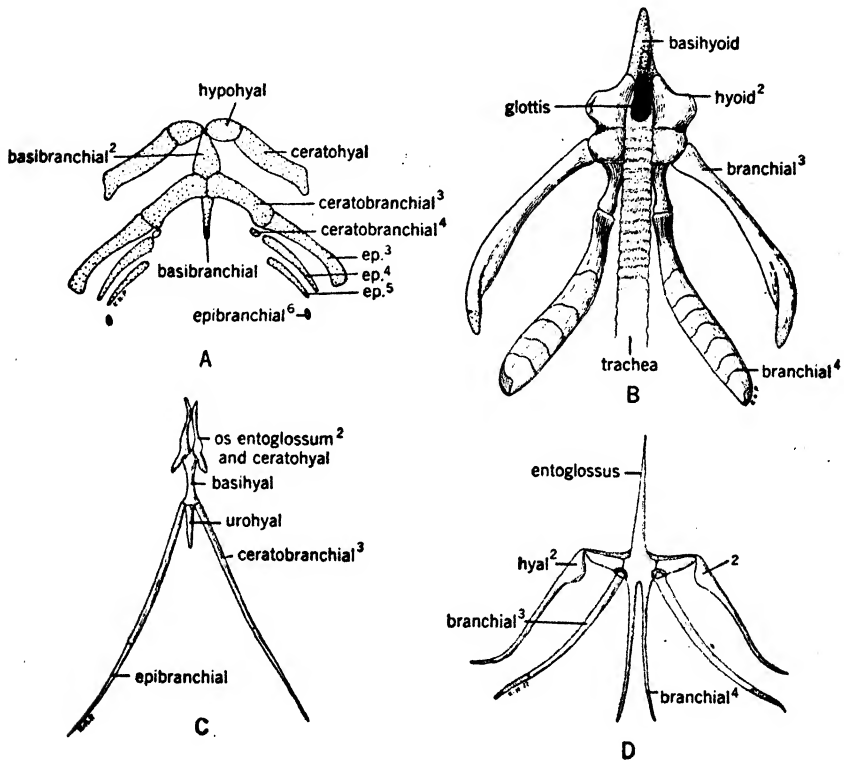


FIG. 128. Hyoid structures. A, *Necturus*; B, *Amyda spinifera*; C, Bird (*Sialia s. sialis*); D, lizard (*Holbrookia maculata*). Figures represent the number of the arch.

Visceral Arches of Birds

The visceral skeleton of the bird (Fig. 128) is considerably reduced and contains remains of the second (hyoid) and third (first branchial) arches. The hyoid consists of a median entoglossus with processes extending laterally. A median basihyal extends posteriorly to join the long horns extending backward, which consist of the paired ceratobranchials and epibranchials of the third visceral arch. A median basibranchial extends posteriorly between the horns of the third arch.

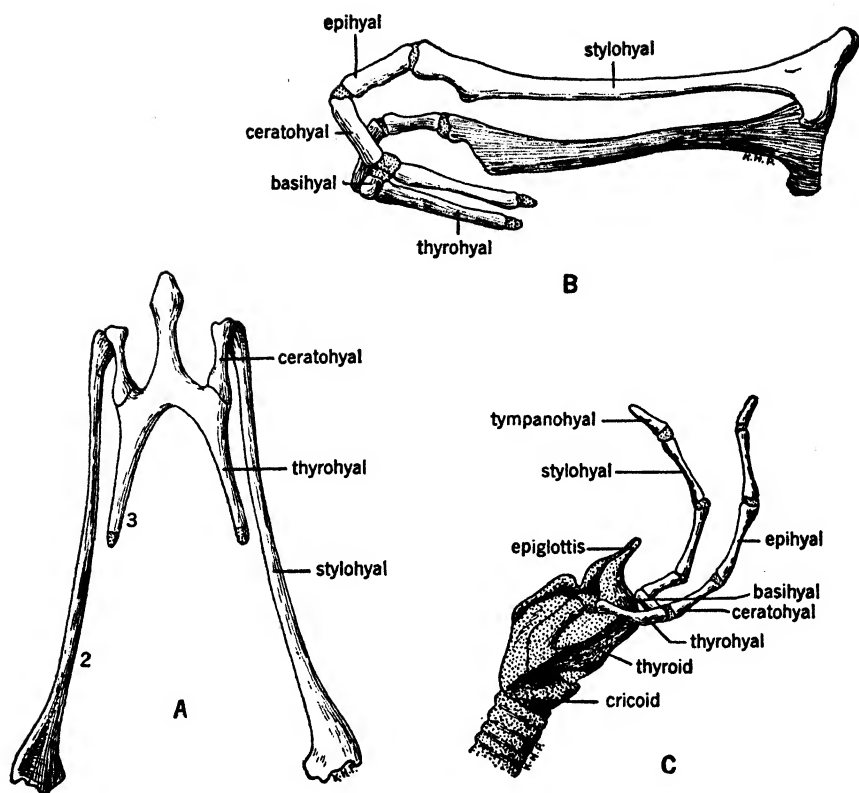


FIG. 129. Hyoid structures of mammals. *A*, horse; *B*, deer; *C*, after Jayne, lateral of cat.

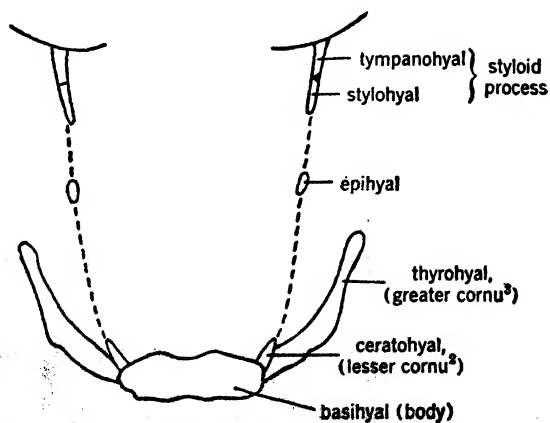


FIG. 130. Human hyoid.

Visceral Arches of Mammals

A mammal, such as the cat or dog, shows a fully developed hyoid structure (Fig. 129), consisting of a central bar, the body (basihyal), from which extend two pairs of horns. The anterior horn consists of four bones, the ceratohyal, epihyal, stylohyal, and tympanohyal. The posterior horns consist of a single pair of thyrohyals. The anterior horns and the body are derived from the hyoid or second visceral arch. The posterior horns are vestiges of the third visceral arch.

The hyoids are reduced in many mammals. In the human the anterior horns of the hyoid structure are greatly modified (Fig. 130). The body has a pair of tiny anterior horns (lesser cornu), which represent the ceratohyal. The distal portion, consisting of the tympanohyal and the stylohyal, are detached and fastened to the skull, forming a very slender styloid process. A ligament extends from the styloid process to the ceratohyal and sometimes contains a small ossification representing a vestigial epihyal. The posterior horns (greater cornu) are much larger than the anterior horns and represent the thyrohyal, which is part of the third visceral arch. Some of the cartilages of the larynx may represent vestiges of other visceral arches. The thyroid cartilage seems to be derived from both the fourth and the fifth visceral arches. The epiglottis is possibly a derivative of the sixth visceral arch.

CHAPTER EIGHT

Axial Skeleton (Continued)

Vertebral Column

The notochord appears suddenly in the geological history of animals, with no definite forerunner that has so far been discovered. The ostracoderms were present in the Ordovician period, and we may safely assume that the notochord was present in these forms. In

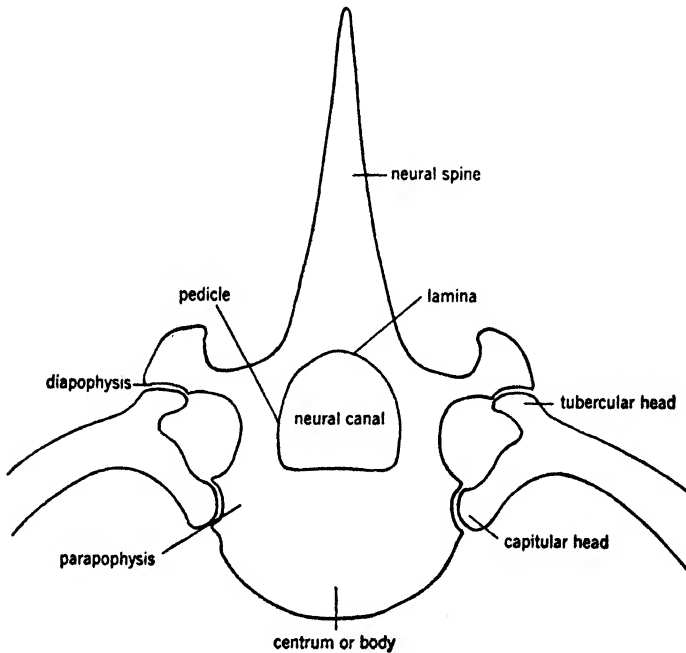


FIG. 131. Diagram of a typical thoracic vertebra.

Amphioxus the notochord is a somewhat elastic rod extending from the tip of the tail to the tip of the snout. It ends near the otic capsule in sharks. Its development appears to be from the endoderm, and, though its form and even its origin may vary, it has a characteristic appearance in all vertebrates and is one of the landmarks of embryological sections, since it is usually vacuolated tissue and unlike any other

structure. Typically the notochord is covered by an inner sheath (*notica interna*) and an outer sheath (*elastica externa*), both of which may be concerned in the formation of the vertebral column.

The unit of the vertebral column is a vertebra, which is the end product of a long series of developments from a condition in which nothing but the notochord is present to the completed vertebra with its specializations. Typically, a vertebra (Fig. 131) consists of a body or centrum formed around the notochord. It is usually heavy, and there are usually some means for making this articulation strong yet flexible. Various devices have been used for this purpose. The centra themselves have been modified at the ends to assist in the joining of the vertebral units. (See Fig. 132.) Acoelous vertebrae are flat at both ends of the centrum; procoelous are those in which the anterior end of

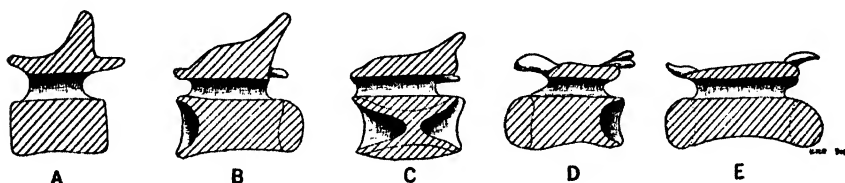


FIG. 132. Types of centra. A, acoelous; B, procoelous; C, amphicoelous; D, opisthocoelous; E, biconvex.

the centrum is concave; opisthocoelous, those in which the posterior end of the centrum is concave; amphicoelous, in which both ends of the centrum are concave (Fig. 132). Some vertebrae have both ends of the centrum with distinct convex knobs. Pads of cartilage are interposed between the vertebrae. Dorsal to the centrum, the neural canal for the passage of the spinal cord is roofed over by the neural arch composed of the dorsal lamina and lateral pedicles (Fig. 131). A neural spine may be present for the insertion of muscles. Tail vertebrae of fishes have a ventral haemal arch for the blood vessels extending to the tail, and may have a haemal spine. The articulation is further strengthened by the development of special processes, the pre- and postzygapophyses, which form an interlocking yet flexible link between two vertebrae. A pair of prezygapophyses is developed on the neural arch with their articular faces pointing dorsally; the postzygapophyses are developed at the posterior end of the vertebra with their articular faces pointing ventrally. The postzygapophyses of one vertebra rest on the articulating face of the prezygapophyses of the vertebra posterior to it (Fig. 133).

Snakes and some reptiles develop a third pair of processes, a zygantrum and a zygosphen, the zygantrum being on the posterior region of the neural arch, with the reciprocal structure, the zygosphen, on the

AXIAL SKELETON (Continued)

rior region of the neural arch. These seem to be necessary because the demand for strength, especially in the pliable column of the snakes. The thoracic vertebrae have large processes on the neural arches

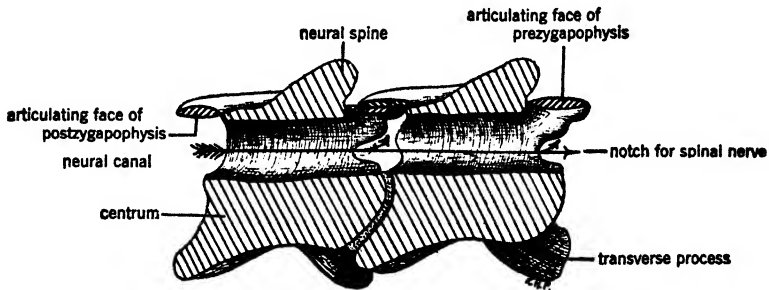


FIG. 133. Sagittal section of two articulated vertebrae.

and centra for the articulation of the ribs. A dorsal diapophysis supplies the articulation (costal facet) for the tubercular head of the rib, and the ventral parapophysis (demifacets) supplies the articulation for

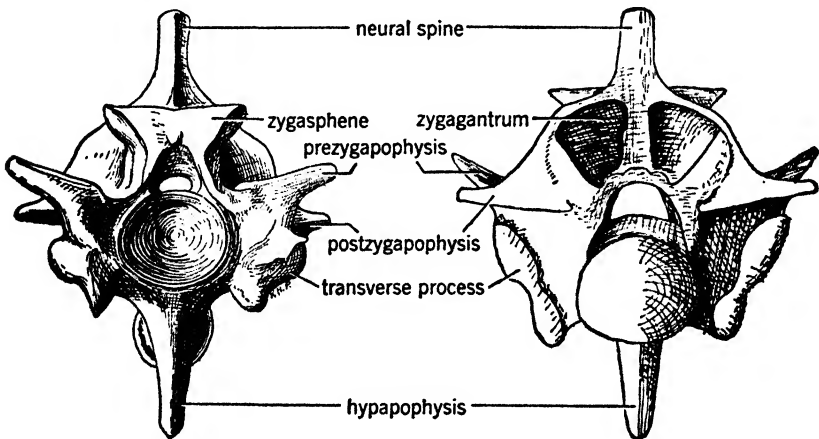


FIG. 134. Vertebra of python: A, anterior; B, posterior.

the capitular head. Lumbar vertebrae have these processes fused to form a transverse process, giving them a characteristic form. Cervical vertebrae of birds and some reptiles may have a median ventral ridge on the centrum, the hypapophysis (Fig. 134).

Embryological Development

Embryologically, vertebrae arise from the sclerotomes, which migrate so as to surround the notochord and nerve cord. Each pair of sclero-

tomes gives rise typically to four major pairs of cartilages known as arcualia (Figs. 5, 135); an anterior dorsal pair above the notochord, the basidorsals; an anterior ventral pair below the notochord, the basiventrals; a posterior dorsal pair, the interdorsals; and a posterior ventral pair, the interventrals (Figs. 5, 135). The basidorsals and the basiventrals give rise respectively to neural and haemal arches. The interdorsal and interventral arcualia give rise to the intercalary plates of the Chondrichthyes. Their derivatives in the higher vertebrates are not clear.

The centrum is formed about the notochord in several ways. In some vertebrates, such as the Chondrichthyes, arcualia invade the

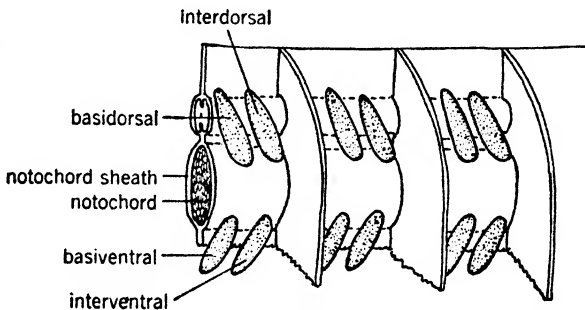


FIG. 135. Diagram of arcualia about the notochord.

sheath of the notochord, forming the centrum. In higher vertebrates, masses of mesenchyme seem to form about the notochord and give rise to the centrum. Two elements, the hypocentrum below and the pleurocentrum above usually enter into centrum formation. These seem to be related to the interdorsals and interventrals, but the relationship is not clear. Although these arcualia usually appear only in embryonic development, they appear as undifferentiated arcualia in the adult vertebral column of the sturgeon. Thus vertebrae are formed from a number of parts, and the failure of some parts to form causes many of the variations found in the vertebrae of different groups.

In some vertebrates the centra are formed by both hypocentrum and pleurocentrum, and in others the centra are formed from only one of these elements. In such cases the other element may appear as an intravertebral disc, an extra centrum (as in some cases of diplospondyly), or it may form extra vertebral structures, such as chevron bones (Figs. 136, 139 B). These appear as ventral arches on the caudal vertebrae and are known as haemal arches in the fishes, and in the rest of the vertebrates, as chevron bones. These bones appear on the tails of many of the tetrapods, especially those with long tails. They are quite common in the long-tailed mammals. The relation of the

haemal arch of the fish to the chevron bone of the tetrapods is not at all certain, and they may have an entirely different origin.

Formation of Vertebrae.

Monospondyly is a condition of the vertebrae in which the anterior and posterior elements of neighboring somites fuse and form a ver-

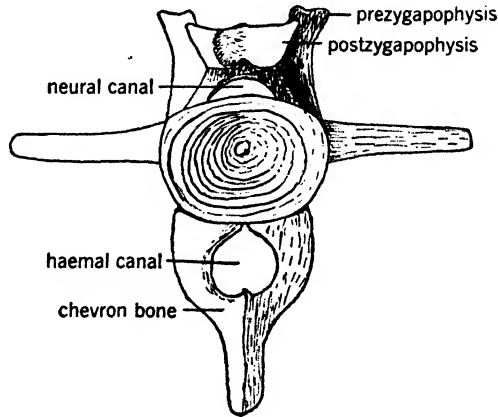


FIG. 136. Posterior view of third caudal vertebra of *Didelphis* (opossum).

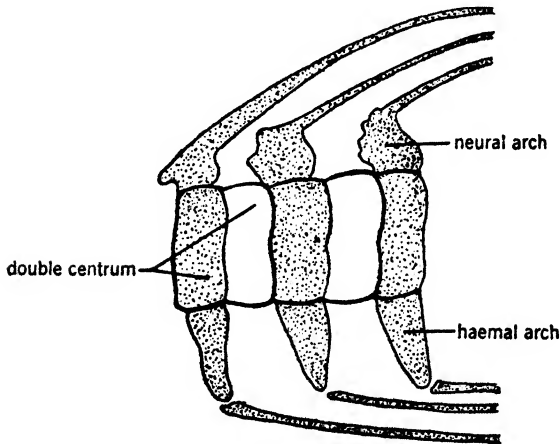


FIG. 137. Caudal vertebrae of *Amia* showing double centra.

tebra between the somites. Occasionally, as in the tails of some reptiles, failure of the arcualia to fuse with those of the adjacent somite results in a diplospondylous vertebra. When the arcualia fail to fuse, each arcuale forms a separate vertebra and thus, two vertebrae lie within one somite. This condition exists in the tails of many lizards and causes the tails to be very brittle. Diplospondyly (Fig. 137) also

occurs in the tail of *Amia* and other fishes. These have a different type of diplospondyly in which the hypocentrum and the pleurocentrum form two separate centra for each vertebra, although only one bears neural and haemal arches.

Cyclostomes

The cyclostomes present important features in the development of the vertebral column. The notochord persists as the main element

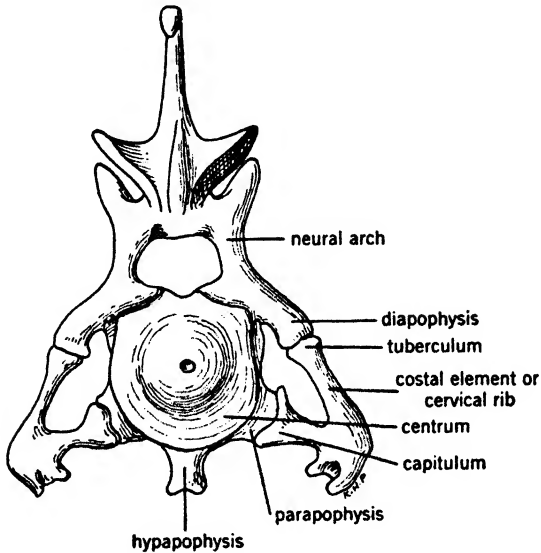


FIG. 138. Fourth cervical vertebra of crocodile showing cervical ribs.

in the axial skeleton, and in the myocommata tiny dorsal cartilaginous riders develop that arch over the nerve cord, and corresponding ventral riders form haemal arches protecting the blood vessels. These small cartilages are the only evidence of vertebrae. No centra are developed to unite these arches, and the notochord is not constricted in any way.

Fishes

The vertebral column of all fishes, including the Chondrichthyes and Osteichthyes, have only two regions, the trunk and the tail. The caudal vertebrae are characterized by haemal arches, which spread in the trunk to give rise to processes that form articulations for the pleuroperitoneal ribs. The sharks develop the vertebral column into a series of cartilaginous parts that may be calcified or hardened. Neural and haemal arches are developed with intercalary arches between. The centrum is formed in two ways with characteristic

effects on the notochord. The asterospondylous vertebrae are formed by invasions of cartilage into the tissue of the notochord, and the cyclospondylous vertebrae are formed around the cord, which is constricted so that the finished centrum shows concentric rings. *Acipenser* and many of the fossil crossopterygians, such as *Caturus*, show the elements of the vertebrae clearly separated. These elements are joined together in the vertebrae of the teleosts, each vertebra being well formed with a centrum, a neural arch, and (in the tail) a haemal arch. Means of interlocking the vertebrae have also appeared and are present in the teleosts. Double centra (diplospondyly) are found in the tail of *Amia* (Fig. 137), where the anterior and the posterior halves of the centrum do not unite.

Amphibians

The vertebrae of the early extinct forms showed many variations as the centra originated in several ways. In modern amphibians the centra are derived from hypocentra and the intravertebral discs from the pleurocentra. The vertebral column, in general shows a progressive growth and development.

The axial skeleton is consolidated, the parts reduced, and the vertebrae better formed, losing their vacuolated appearance and roughness. All the series of bones that supported the median fins are gone, and the neural spines are smaller in proportion and shorter. The vertebrae are better locked together by pre- and postzygapophyses. The vertebral column shows the beginning of the differentiation into cervical, trunk, sacral, and caudal regions which are characteristic of the tetrapods. The sacral region of the amphibians is formed by the modification of one vertebra to articulate with the pelvic girdle. The cervical or neck region is initiated by the specialization of the most anterior vertebra to support the skull.

Reptiles

The reptiles have five regions fairly well differentiated, with cervicals, thoracics, lumbar, sacral, and caudal. The cervicals, however, still retain ribs, the thoracics are modified for rib articulations; and the sacral are acquiring better articulations for the pelvic bones, and, though the number is still small (two or more), the typical sacrum is being approached in form. The centra of reptiles and higher vertebrates is apparently derived from the pleurocentra, and intravertebral discs are derived from the hypocentra. Chevron bones (Figs. 136, 139), extending ventrally between the caudal vertebrae, enclose the caudal vessels. The origin of the chevron bones is uncertain, as some believe they are derived from haemal arches and others think that

they are derived from misplaced hypocentra. In *Sphenodon*, the hypocentra form small pieces between the caudal centra, and these are continuous with the chevron bones. The dinosaurs, with a bipedal gait

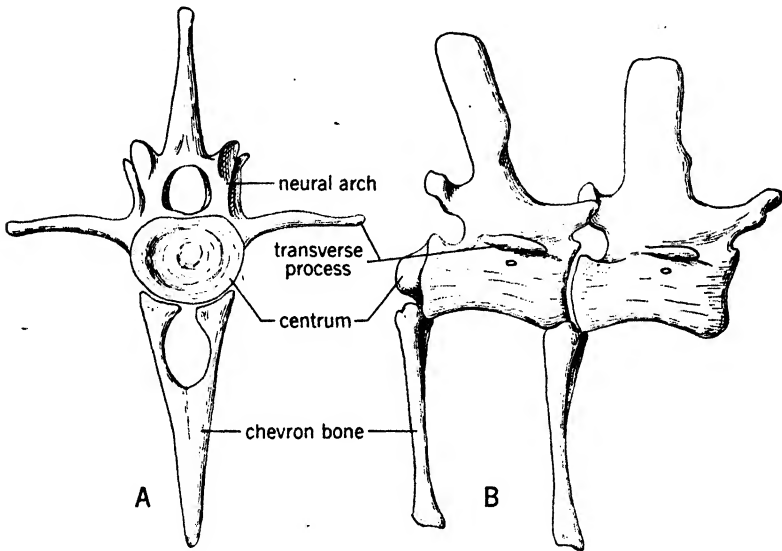


FIG. 139. A, Posterior view of 8th caudal vertebra of crocodile; B, 8th and 7th caudal vertebra of crocodile.

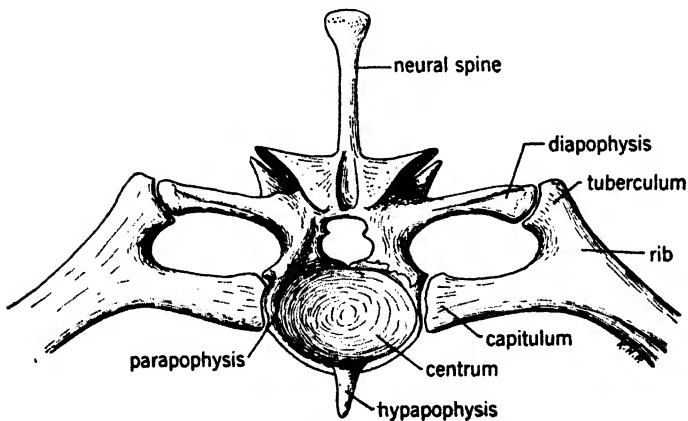


FIG. 140. Fourth thoracic vertebra and attached ribs of crocodile.

and hopping legs, developed a sacral region resembling that of the birds. The pterodactyls paralleled the birds in joining a number of the vertebrae to form a sacrum. Snakes develop a very motile skeleton in which there is great freedom of motion yet the strongest union

of the individual vertebrae by extra processes, the zygantra and zygosphenes (Fig. 135).

The vertebral column is fairly well differentiated into five regions, in the lizard *Sceloporus*. The vertebrae are procoelous (Fig. 132) and are provided with pre- and postzygapophyses. The cervicals, seven in number, consist of a ring-like atlas, an axis with a prominent odontoid process, and five cervicals supplied with ribs. The last two have much longer ribs, which are close to the sternum but not articulated with it. The thoracic vertebrae are not well differentiated from the lumbar, and all have ribs. Those of the thoracic region have longer

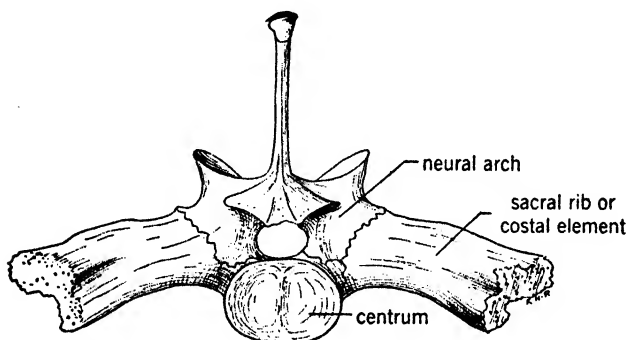


FIG. 141. Posterior view of sacral vertebra of crocodile.

ribs, and five are connected with the sternum by sternal ribs, three to the sternum proper and two to the xiphoid process. The ribs of the posterior end of the series become smaller as the sacrum is approached. The two sacrals are ankylosed together, forming a stable articulation for the ilium. The caudals are over forty in number, a part of them being supplied with Y-shaped chevron bones which articulate with the ventral side. The caudal vertebrae are diplospondylous which causes a loose attachment of the vertebrae, permitting disarticulation in time of danger to the animal.

Birds

The modern bird has a highly specialized vertebral column in which the various parts are well adjusted to the needs of flight. The vertebral column of the chicken shows the typical structures of a flying bird.

The 16 cervical vertebrae of a chicken form a long flexible neck. The atlas, the first cervical, is ring-like and provided with a facet for the condyle of the skull. The axis, the second cervical, is small, ribless, and provided with an odontoid process for the articulation with the atlas. The remaining cervicals have small, fixed ribs, except

the last three, which are free. The centrum is long in the typical cervical, with a peculiar saddle-shaped articular surface at the posterior end. The neural spines are present on only a part of the cervicals.

The five thoracic vertebrae become a part of the rigid region developed in the bird body. The first three fuse with the last cervical,

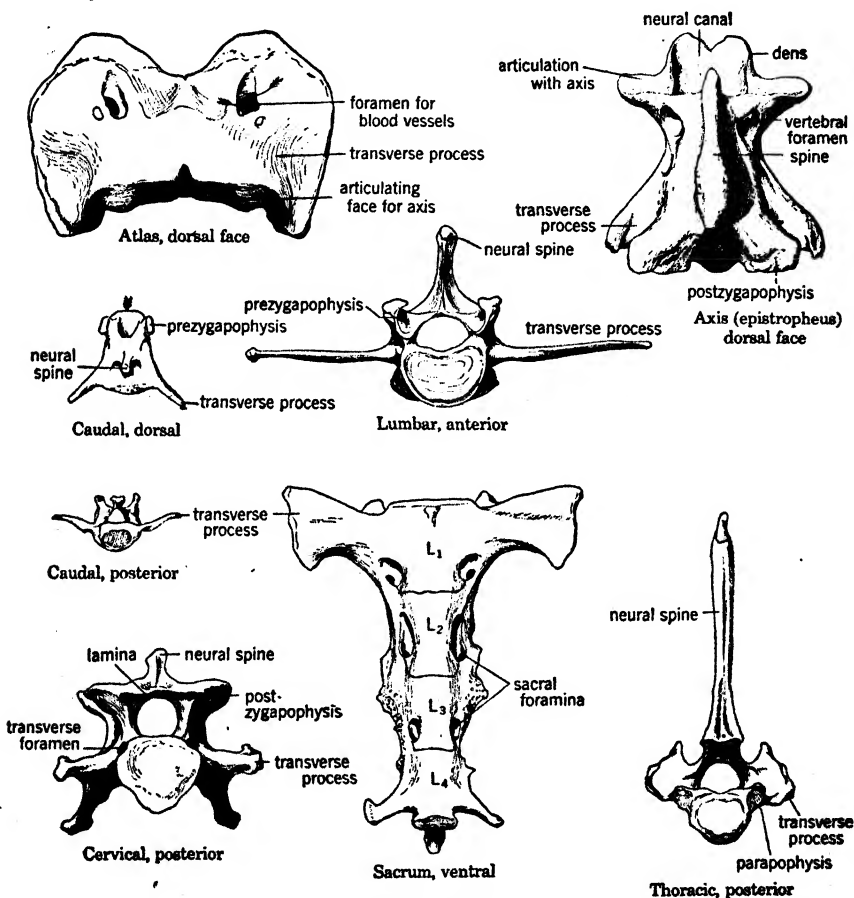


FIG. 142. Vertebrae of a sheep from different regions of the vertebral column.

making a solid section, with joined neural spines and hypapophyses. The fourth thoracic is free, and the fifth, or last, joins the lumbar to assist in forming the synsacrum. The lumbar, sacral, and a part of the caudals are fused together, making a solid articulation for the ilium. It is difficult to differentiate these regions, but it is probable that the sacral number two as in the reptiles. The lines of demarcation are clear between the individual vertebrae, although their centra

are joined and fused. The free caudals, four or five in number, with a fused series, the pygostyle, terminate the tail. This region is very important in flying birds, since it carries the tail feathers and is valuable in steering. The vertebral column of the ratites or running birds is not as rigid as in the flying birds. The thoracic vertebrae tend to

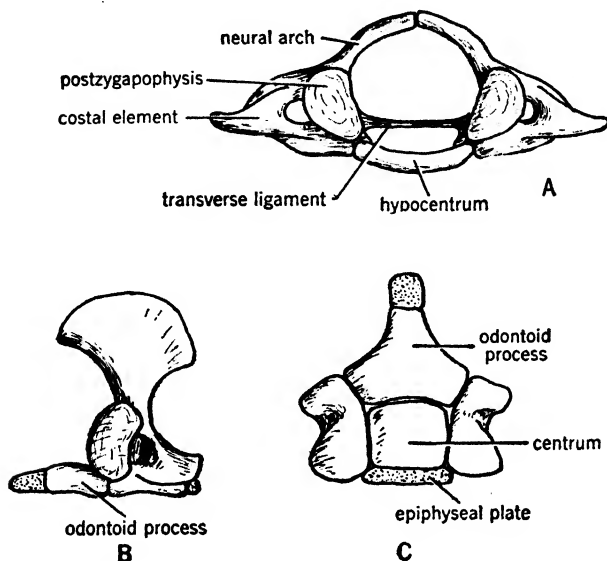


FIG. 143. Atlas and axis (epistropheus) of newborn kitten. A, posterior view of atlas; B, lateral, left side of axis; C, ventral side of axis.

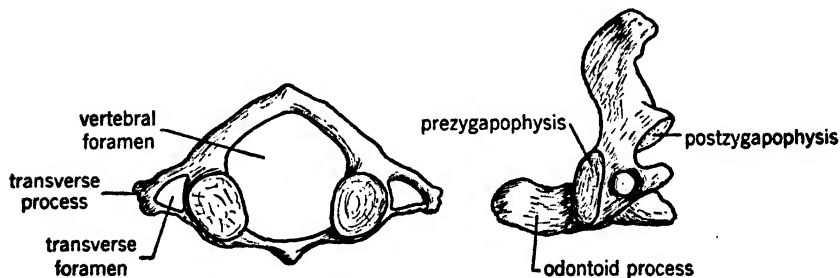


FIG. 144. Human atlas and axis.

be free although the lumbar, sacral, and part of the caudals are fused in a synsacrum. The caudal vertebrae are more numerous and tend to be more loosely articulated.

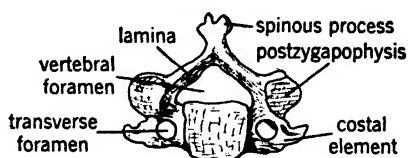
Mammals

The vertebral column of mammals is divided into well-defined regions. The number of vertebrae in each region is fairly definite

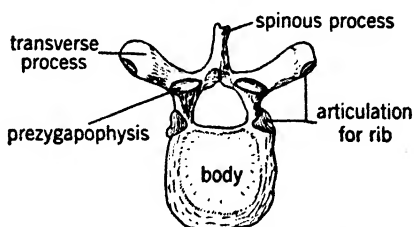
except in the edentates and cetaceans. The typical arrangement is as follows: cervicals 7, thoracics 12-13, lumbers 5-6, sacrals 2-5, caudals variable (4 in man). (See table, page 199, for variations in numbers of different regions.) The vertebrae of each region are differentiated by special characters.

The typical cervical vertebra (Fig. 142) consists of a centrum, a neural arch and spine, and articulating processes. The articulating surface of each prezygapophysis faces dorsally (up), and that of the postzygapophysis ventrally (down). The transverse process on each side of the centrum has a foramen for the vertebral artery at its base which is formed by the fusion of a vestigial cervical rib, enclosing the vertebral artery. The neural arch is shorter than the centrum, so that the spinal cord is not completely roofed over, thus allowing more movement. The ends of the centrum are acoelous, or flat, in most mammals (Fig. 132) but ungulate cervicals are opisthocelous. The first two vertebrae, the atlas and axis, are the most specialized (Fig. 142, 143). The atlas is ring shaped and has lost most of its centrum, only a slender bar formed by the hypocentrum remaining. It has two facets on the anterior face that articulate with the condyles of the skull. Conspicuous wing-like processes make the atlas distinctive. The axis or epistropheus is characterized by a large neural spine and by an odontoid process derived from the detached pleurocentrum of the atlas (Figs. 142, 143, 144). The odontoid process extends forward from the centrum into the atlas.

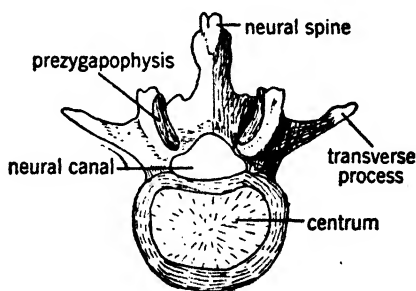
The thoracic vertebrae (Figs. 142, 145), are usually marked by strong dorsal spines, the first being almost perpendicular, and the rest inclining gradually more to the posterior. The facets on the



Human cervical, posterior view



Human thoracic, anterior view



Human lumbar, anterior view

FIG. 145. Human vertebrae.

anterior and posterior regions are for the capitular head, and those of the transverse process are for the tubercular head of the ribs.

The lumbar gradually increase in size from the first to the last. Their spines are often inclined anteriorly with a gradual increase of

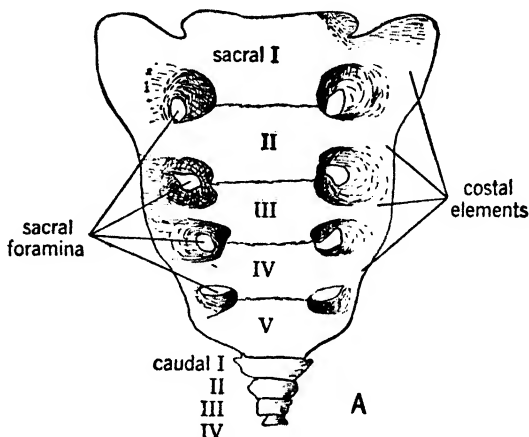


FIG. 146. A. Anterior or pelvic surface of the human sacrum and coccyx. $\times \frac{1}{3}$.

the inclination as the last vertebrae are reached. The centra are large, much heavier than in the thoracics, with conspicuous transverse processes. On some, as in the rat, the hypapophyses, median flanges on the ventral surface of some of the lumbar, are similar to those developed in birds and reptiles. Some interesting devices are developed in the lumbar region of the ungulates, particularly in the artiodactyls, where the pre- and postzygapophyses are shaped so as to interlock and thus strengthen this region.

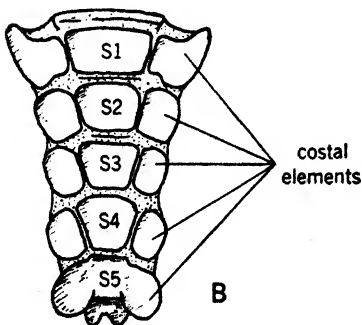


FIG. 146. B. Ventral view of sacrum of a newborn kitten showing vestigial ribs. s1-s5, centra.

The sacral region (Fig. 146) includes a number of vertebrae, varying from two to thirteen. Each of these is fused laterally to a short vestigial sacral rib (Fig. 146). There is a tendency for this series to coalesce in the adult to form a single piece, but the outlines of the individual vertebrae are usually definite, as shown by the suture lines.

The sacrum varies greatly in shape, since it is very closely correlated with the type of pelvis attached to it.

The vertebrae of the tail become modified toward the end, until

nothing but the centrum remains. Except in mammals that make use of the tail as a prehensile organ, the development of pre- and post-zygapophyses is weak. The neural arch is carried on the first part of the series but is gradually reduced and finally lost entirely. Chevron bones are present on the tails of a number of mammals including monotremes, marsupials, Xenarthra, rodents, cetaceans, carnivora, and primates (Fig. 136).

THE NUMBER AND DISTRIBUTION OF THE VERTEBRAE IN
SOME VERTEBRATES

	Cervicals	Thoracics	Lumbars	Sacrals	Caudals	Total
Man	7	12	5	5	3-4	32-33
Cat	7	13	7	3	18-25	48-53
	(thoracics + lumbars)					
<i>Bradypus</i> (three-toed sloth)	9	20		6	11	36
Opossum	7	13	6	2	19-35	47-63
Chicken	16	5	8	2	9+	40+
	pygostyle pygostyle					
	(Synsacrum consists of 1 thoracic, 8 lumbars, 2 sacrals, 4 caudals)					
<i>Alligator</i>	8	11	5	2	40+	67+
<i>Python</i>	(Regions not clearly differentiated)					435
	(thoracics + lumbars)					
<i>Necturus</i>	1	18		1	23+	43+
<i>Cyprinis</i>	(Body) 17				17	34

Ribs

Ribs appear early in fishes; small chondral ribs are found in the Chondrichthyes. Two kinds of ribs, both of chondral origin, are common in many fishes and often appear together on the same vertebra. These are best known as dorsal and ventral ribs (Fig. 147).

The dorsal ribs appear as intermuscular structures in the septa between the myotomes where these septa meet the septum separating the epaxial and hypaxial muscles. They have long been thought to be homologous to the ribs of the tetrapods but the studies of Emelianov have indicated that this kind of rib is restricted to fishes. Some fishes even multiply these ribs. In cyprinids (minnow family) and catostomids (sucker family) there are a pair of both dorsal and ventral ribs for each vertebra from the head to the tip of the tail. In these fishes the dorsal ribs are often branched to resemble a fagot and seem to lie above the septum separating the hypaxial and epaxial muscles.

Ventral ribs are often called pleuroperitoneal ribs (Fig. 147). They lie in the myoseptum just under the peritoneum of fishes. They apparently are the only ribs possessed by the tetrapods, where they move farther into the myoseptum. In fishes they have been called haemal ribs on the assumption that they originate as continuations of the haemal arches, which split and spread in the trunk region. However, the fact that some of the teleost fishes have ventral ribs on the caudal vertebrae, which also possess perfect haemal arches, indicates that

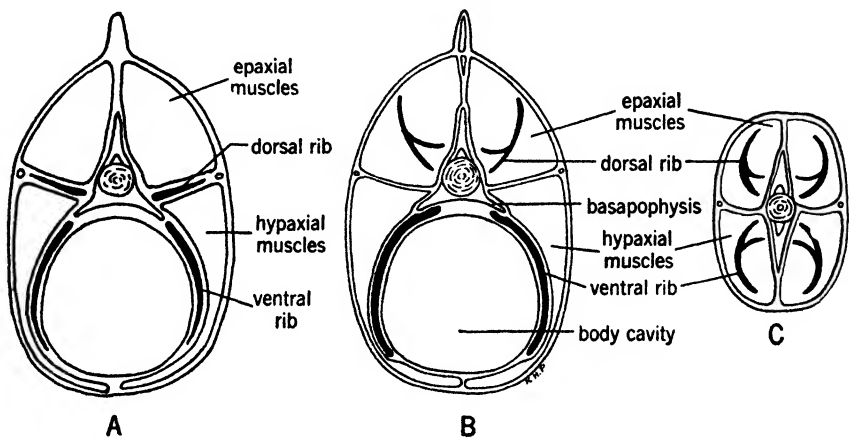


FIG. 147. Diagrams of fish ribs. A, typical arrangement of dorsal and ventral ribs; B, ribs in trunk region of carp; C, ribs in caudal region of carp.

they are not related to the haemal arches (Fig. 147). In fishes the haemal arches in the trunk region spread and form basapophyses to which these ribs articulate. When present in the caudal region of fishes, they may articulate on the vertebrae as they do in the higher vertebrates.

Originally extending along the whole length of the body, pleuroperitoneal ribs become more and more restricted in the higher animals, until they are developed only in the thoracic region in mammals. The ribs of fishes are attached low on the centra (Fig. 147), and their ends are not connected at the mid-ventral line, since no sternum is present. In amphibians they are a little more varied and are generally bicipital, having a capitular and a tubercular head for articulation with the vertebrae; but they are not connected with the sternum. The urodeles have a series of ribs extending along the body, but the ribs are generally short and of little importance. The single cervical vertebra has no rib. In reptiles the sternum is well developed, and the ribs are attached to it for the first time to form the complete

thoracic basket. There is still a tendency, however, for the ribs to extend the whole length of the body. Vestiges of ribs can be seen in the neck (Fig. 138) and other regions. Generally the ribs are bicipital (two heads) in reptiles. Uncinate processes, joining adjacent ribs, are present in *Eryops*, alligators, and *Sphenodon*. The ribs of turtles become specialized and ankylosed with dermal plates to form the carapace. Furthermore turtles have their pelvic and pectoral girdles inside their ribs. In birds the cervical ribs although vestigial can be clearly seen. In ratites the last cervical ribs are not fused to the vertebrae but hang free. The thoracic ribs of flying birds usually bear uncinate processes. Mammals have only fully developed thoracic ribs, which are articulated with the sternum by cartilaginous extensions (sternal ribs) except for a small number of floating ribs. The ribs are bicipital and articulate with the vertebrae.

The fully developed mammalian rib is a bony vertebral rib, which has a long shaft or body ending dorsally in two articular processes, the head or capitulum articulating on the demifacets between two centra and the tuberculum articulating on the costal facet of the transverse process. The part of the vertebra between the capitulum and the tuberculum is the neck. Ventrally the shaft of the rib ends in a cartilaginous sternal rib articulating with the sternum. The posterior ribs generally fail to connect with the sternum.

Vestiges of ribs can be found in many of the other regions of the mammalian vertebral column. Cervical ribs (Fig. 145) are represented by the fused costal elements of the cervical vertebrae. This element represents only the capitulum, tuberculum, and neck of the cervical rib. Lumbar ribs are represented by mere vestiges consisting of a cartilage fused to the tip of the transverse processes. Sacral ribs (Figs. 143, 146) are present as the fused lateral wings of the sacrum and appear as separate elements in the fetus.

Mammals have ordinarily from twelve to fifteen pairs of thoracic ribs, although some Cetacea have as few as nine, and some sloths have as many as twenty-five. Elephants, horse, and some other ungulates have eighteen to twenty.

Sternum

With the development of the ribs, the circle of bone around the body was completed in the thoracic region except along the mid-ventral line. The development of the sternum in the tetrapods completed this gap. The sternum not only supplies the support needed for the shoulder girdle but also provides an area for the insertion of some of the muscles of the fore limb. Its origin appears to be from the fused ends of the

ribs. It is not found in the elongate, snake-like forms, nor is it clearly developed in amphibians. In *Cryptobranchus* a heart-shaped cartilage,

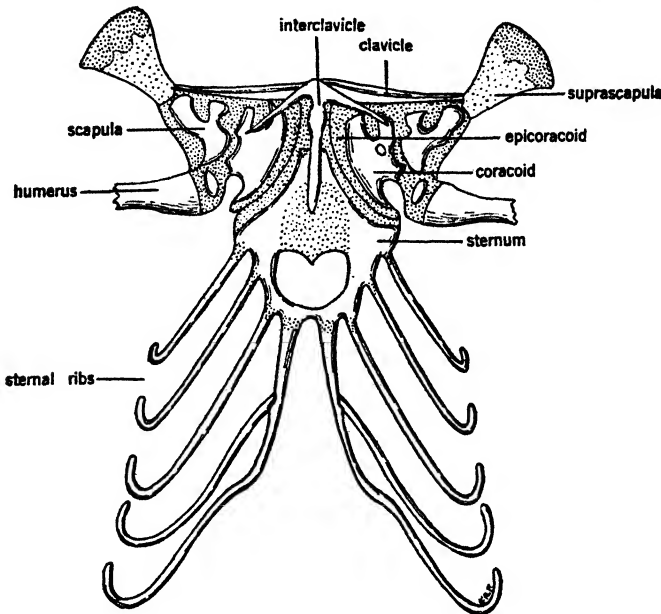


FIG. 148. Sternum and shoulder girdle of lizard, *Holbrookii*.

articulating with the two coracoids, forms a central element, but it is not attached to ribs. In *Rana*, a higher development with a presternum and xiphisternum appears, but it seems related to the shoulder girdle. No ribs are attached to it in the amphibians. In reptiles (Fig. 149) there is the beginning of connection between the ribs, and the first definite appearance of a true sternum.

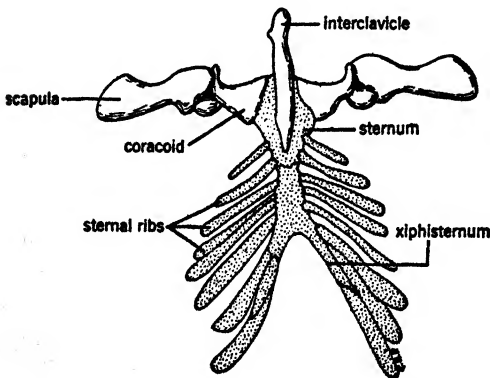


FIG. 149. Sternum and shoulder girdle of alligator.

The lizard *Holbrookii* (Fig. 148) has four ribs attached, and the coracoids are well articulated. The cartilaginous sternum of the lizard *Sceloporus* is well developed and is connected through three sternal ribs with the first three thoracic vertebrae. A large heart-shaped fontanelle forms a conspicuous opening in the cartilage. The large T-shaped interclavicle extends ante-

riorly along the medial line and supplies an articulation for the two clavicles, which in turn tie the shoulder girdle to this structure. The sides of the anterior region have grooves for the articulation with the coracoids.

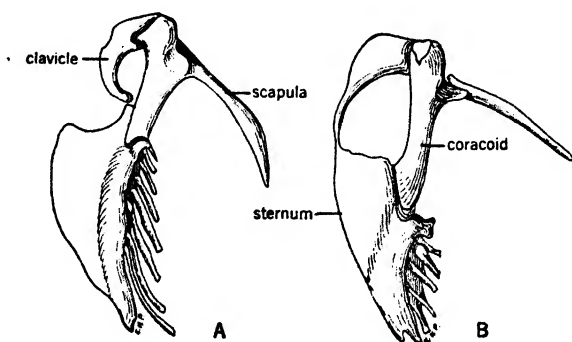


FIG. 150. Sternum and shoulder girdle. A, eagle; B, pelican.

Birds have a striking sternum, which offers excellent attachment for the large pectoral muscles used in flight. The sternum (Fig. 150) is a large bone, covering the ventral side of the body and projecting posteriorly so as to protect the whole abdominal wall. It is convex on its ventral surface and somewhat narrowed at the posterior end, with a xiphoid process along each side. The median line is drawn out into a keel, which is used for the attachment of the flight muscles. The sternum of running birds lacks a keel and is reduced in size. In cranes and swans a part of the trachea is coiled within the sternum, showing the double origin of this now single structure. The bracing in birds is perfect, because of the articulation of the coracoids and the close connection with the clavicles.

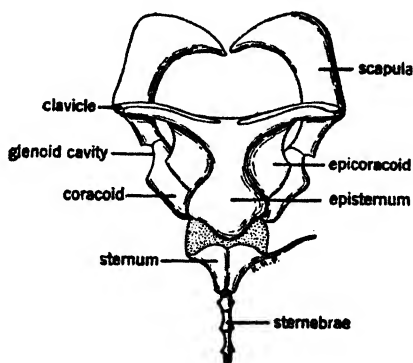


FIG. 151. Sternum and shoulder girdle of duckbill (*Ornithorhynchus*).

The sternum of mammals is somewhat simplified except in the monotremes (Fig. 151), where the reptilian appearance remains. In Mammalia (Fig. 152), a number of sternalia or sternbrae are developed, as in the rat, where there are a presternum, six sternalia, and a xiphisternum. In man the sternbrae fuse early in life, forming three elements, the manubrium, xiphoid, and xiphisternum, all partially ossified as a rule.

Episternum (interclavicle)

The episternum (Figs. 148, 149) is a small median element applied to the ventral side of the sternum. It is found in amphibians and reptiles

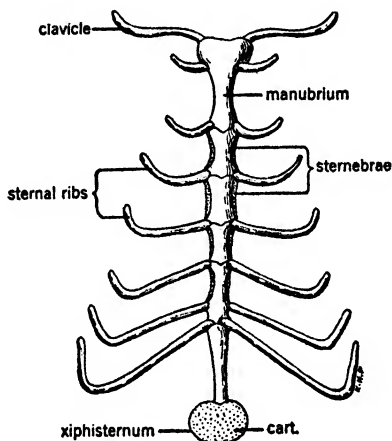


FIG. 152. Sternum of rat.

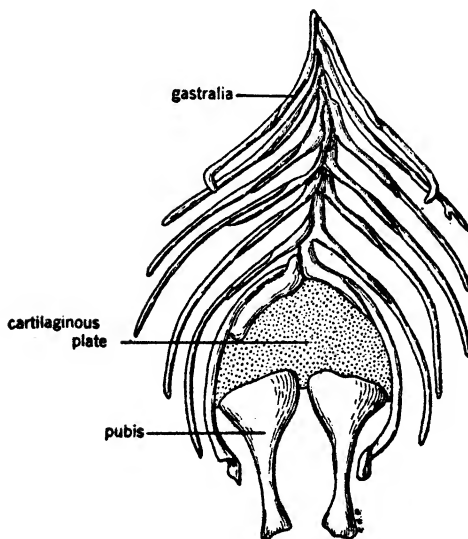


FIG. 153. Gastralium or abdominal ribs of alligator.

but is not represented in mammals, except in monotremes (Fig. 151). It is well developed in the Lacertilia, Crocodilia, and other reptilian forms. It is probably a part of the pectoral girdle, where it is described as an interclavicle.

Gastralia

Splint-like dermal bones known as abdominal ribs (Fig. 153) or gastralia were developed in the extinct amphibians and are present as conspicuous skeletal parts in Crocodilia, *Sphenodon*, and other reptiles. They were also present in *Archaeopteryx*, the earliest bird. They cover the region between the sternum and pelvis, and protect the soft parts not protected by ribs. They probably enter into the formation of the plastron or ventral part of the turtle's carapace.

CHAPTER NINE

Appendicular Skeleton

The appendicular skeleton consists of the bones of the pectoral and pelvic girdles and the attached paired appendages. The appendages in the fishes are the paired fins and in the tetrapods are the limbs. The paired fins arose early in the fishes, and, in the transition to a land life, developed into the pentadactyl appendages of the tetrapods. Girdles are the skeletal foundation within the trunk for the attachment and support of the limb. Paired appendages and girdles are present in all vertebrates above the Agnatha, except those few forms, such as the Gymnophiona and the Ophidia, which originally had legs but have lost them. The first vertebrates (Agnatha) apparently did not have paired appendages, and there is much speculation as to their subsequent origin.

Origin

Three older theories have been suggested for the origin of fins: the gill-arch theory of Gegenbaur; the finfold theory advanced by Thacher and elaborated by several European writers; and the external-gill theory of Kerr. Gegenbaur and his followers assumed that gill arches slipped along the body and developed into the pectoral and pelvic girdles and fins. Little evidence has been found to support this assumption, and few fossil or modern fishes have the type of fins that would result from such an origin. The fins themselves, according to this theory, would have come from the branchial rays, thus having a median axis with small pieces of material along the sides, somewhat similar to those of *Neoceratodus*.

The finfold theory (Fig. 154) is supported by more positive evidence, although the evidence is not all conclusive. The finfold theory gets its main support from type of fins in embryos, where there is a continuous fold; type of fins in *Amphioxus*, cyclostomes, and in some living fishes; and from the condensation of the nerve supply to the limb buds in the developing fish. According to Thacher, the appendicular skeleton developed in two pairs of primitive folds running along the sides of the body. The more dorsal pair of folds approached

the dorsal line and finally formed a median fold extending the entire length of the body and around the tail to the vent. The ventral pair of folds extended from the head region along the side walls to the vent. These folds were gradually supported by the ingrowth of mesoderm, and finally became fin-like in their basic structure. These folds assisted in keeping the balance and in preventing a corkscrew motion while the animal was moving through the water. It is assumed that the lateral folds were capable of movement at two regions along the sides and that these two centers of action were eventually separated, becoming the anterior and posterior pairs of fins. The lappet-like appendages of the placoderms, *Cladoselache* (Fig. 155), and early elasmobranchs seems to be in line with this theory.

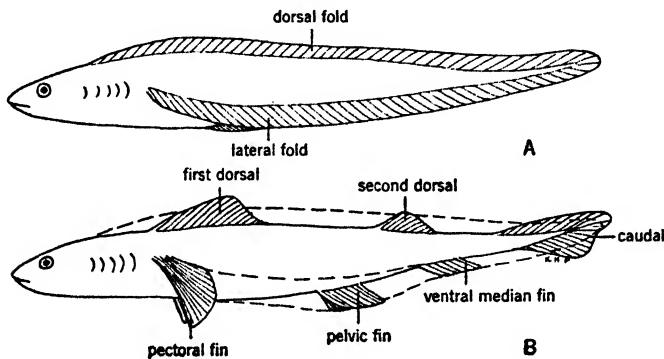


FIG. 154. Diagrams illustrating the finfold theory of the origin of fins. A, continuous folds; B, folds broken up into regions. After Wiedersheim.

A third theory, that of J. Graham Kerr, comes from an embryological study of primitive fishes and dipnoans. It is a modification of the gill-arch theory of Gegenbaur, in that the limb girdles are derived from visceral arches, but it derives the fins and limbs from external gills. The external gills occur in the embryological development of primitive fishes and amphibians. Besides respiratory functions, these external gills may serve as balancers, since they are supplied with a musculature and are capable of movement.

What at first appeared to be a rather simple problem has turned out to be more complex than the early writers anticipated. In recent years a much better understanding of the older fishes has developed, and this supplies a much broader base for solving such problems as the origin and evolution of fins. The knowledge that has been gained of the oldest fishes, such as the ostracoderms and placoderms, has supplied a much better basis for theories that formerly rested entirely on modern living forms or on embryology. Although finfolds are com-

mon in living fishes and appear in many young fishes in developmental stages, it has been found that the oldest fishes above the Agnatha had independent fins both in the median and in the paired series.

Gregory and Raven (1941) state that it seems probable that the dorsal and paired fins of the earliest gnathostomes were not continuous finfolds but nodally placed, compressed ridges, strengthened an-

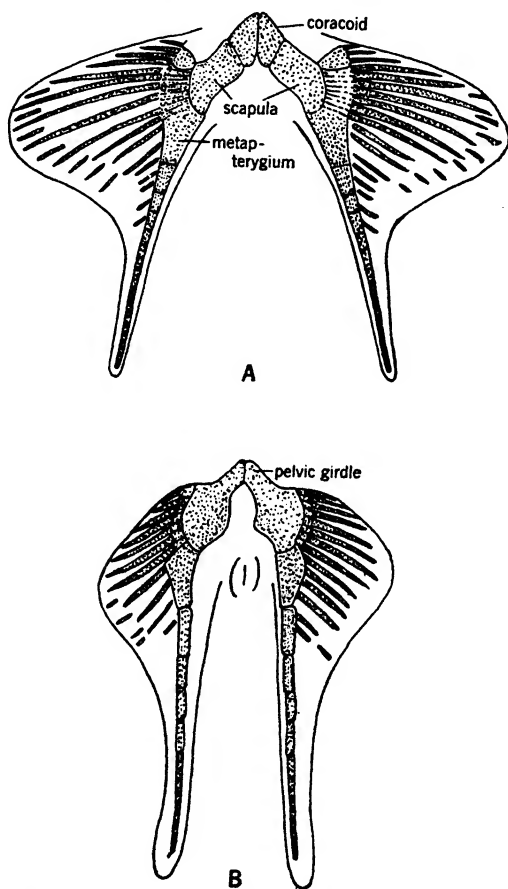
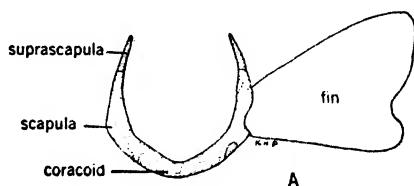


FIG. 155. Girdles and fins of *Cladoselache*. A, anterior fin and girdle; B, posterior fin and girdle. After Jaekel.

teriorly by a concentration of denticles or scales, which often coalesced into fish spines.

Paired appendages appeared early in vertebrates and are practically universal in the subphylum. *Cladoselache* (Fig. 155) had pairs of lappet-like fins with broad bases but not yet connected with internal girdles. The higher elasmobranchs developed a pectoral girdle in the form of a U-shaped piece of cartilage connecting the anterior fin.

Elements were added in higher fishes to tie the pectoral girdle to the skull. These elements, consisting of the cleithrum and several small supracleithra (Fig. 157), are dermal in origin. The scapula and coracoids, developments from the cartilaginous skeleton, which lie along the inner side of the cleithrum, supply an articulation for the fin. The origin of the clavicle is not clear, and in the higher forms it probably consists of both dermal and chondral elements. The interclavicle (Figs. 148, 151), which first appears in the early amphibians, persists in reptiles, birds, and monotremes. There are two bracing elements in the amphibians, the coracoid and the precoracoid. Reptiles add a third, the epicoracoid. Monotremes retain both the precoracoid and the coracoid, but other mammals do not have these as separate elements, retaining only the posterior element which is attached to the scapula as the coracoid process.



Pectoral or Anterior Girdle

The primitive shoulder girdle (Fig. 156) was originally a chondral U-shaped bar with which the pectoral fins articulated. In the primitive bony fishes, this bar gave rise to several chondral bones, such as the scapula and coracoid elements. Simultaneously dermal plates were added to the girdle, forming the cleithrum, clavicle, and several other dermal bones, which became prominent in the teleost shoulder girdle.

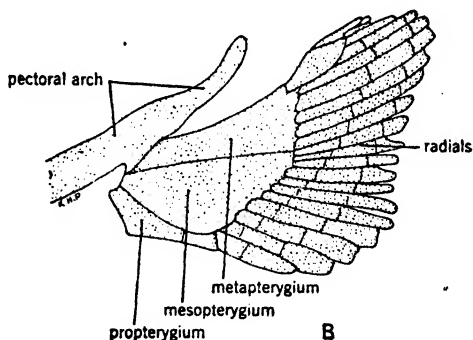


FIG. 156. A, pectoral girdle; B, pectoral fin of *Squalus acanthias*.

The fully developed tetrapod girdle consists dorsally of a pair of chondral scapulae and ventrally of paired chondral precoracoids and coracoids, and dermal clavicles. The union of these four elements is in the general region of the articulation of the limb. The pectoral girdle of man consists only of a scapula, clavicle, and a vestigial coracoid attached to the scapula. The pectoral girdle except in teleost fishes is not directly united to the axial skeleton, although in the higher vertebrates it may fasten ventrally to the sternum.

The shoulder girdle, while always forming an articulation for anterior fin or limb, has other functions also in the fishes. It serves as an

attachment for its regulating muscles. The large dermal cleithrum (Fig. 157) serves as a backwall for the branchial region with its gills and important structures connected with respiration and circulation. In teleosts the cleithrum is usually attached to the skull by a chain of dermal bones, a condition that would appear to be related to the position of the gills and their associated structures. The paired fins with few exceptions are used principally as a balancing organ in fishes and seldom serve to support the body as in tetrapods.

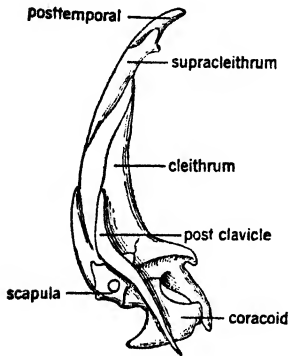


FIG. 157. Left shoulder girdle of teleost (*Ictiobus*).

fuse into one mass. The crossopterygians add a series of dermal elements, the first of which is connected to the skull. The cartilaginous band, though still large in *Acipenser*, is much reduced in *Amia*, where the cleithrum is enlarged to support the scapular elements, and a series of smaller dermal plates connect this cleithrum with the skull. The clavicles, a pair of ventral elements, are found in the older groups of fishes (*Polypterus* and fossil crossopterygians), but in teleosts they are partly replaced by the large bony cleithra, which meet on the mid-ventral line. A modern teleost has very large cleithra (Fig. 157), which are articulated to the skull through several small elements and are braced by a pair of long, thin posteithra or postclavicles. The cartilaginous band has ossified into three pairs of elements in teleosts, a scapular, mesocoracoid, and coracoid.

Amphibians

The girdles of amphibians (Fig. 158) are weak, and the limbs, extending out at right angles, do not properly support the body in walking. This condition of the limbs is somewhat improved in the reptiles, but not until the birds and mammals are reached do the limbs have a position under the body, where they are mechanically most efficient for support.

The early amphibians retained several fish-like structures, among them the large cleithrum. *Cacops*, an early form, had a girdle consisting of a clavicle, interclavicle, cleithrum, and two coracoids. Probably there was a large cartilaginous mass representing the chondral elements. Modern amphibians have a much simpler girdle, *Necturus* having a suprascapula, scapula, precoracoid, and coracoid. The frog has a well-organized girdle, consisting of a suprascapula, scapula, precoracoid process, coracoid, and median interclavicle or episternum.

Reptiles

The early reptiles, such as *Diadectes*, had a girdle much like that of the early amphibians, but in modern reptiles (Fig. 148) there is a complete reorganization. The connection with the sternum is improved, and there is a firm bracing by the clavicle and, generally, a coracoid and epicoracoid. The scapula and suprascapula complete the girdle. The shoulder girdle of *Sceloporus* (Fig. 148) consists of a cartilaginous suprascapula, an osseous scapula, and the coracoids. The coracoids, consisting of a precoracoid, coracoid, and epicoracoid, are not separated by sutures. The alligator (Fig. 149) simplifies the girdle until it consists of only three elements—the suprascapula, scapula, and coracoid.

Birds

Carinate birds have a girdle well developed for flight. Their girdle forms a firm articulation for the wings and is composed of a pair of blade-like scapulae, a pair of heavy precoracoids fused with a pair of coracoids, and a furcula or "wishbone" consisting of a pair of clavicles fused with an interclavicle (Fig. 159 A). The coracoid element is a stout bone articulating distally with the scapula and prox-

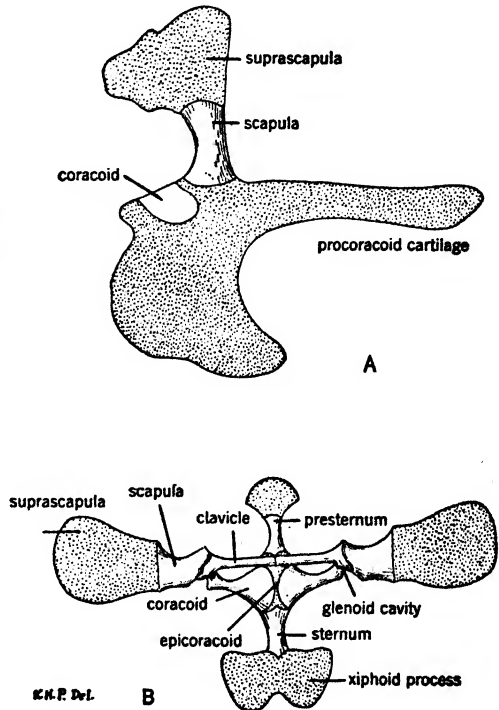


FIG. 158. A, right shoulder girdle of *Necturus*. B, shoulder girdle of *Rana*.

imally with the sternum. The ratites originally developed a similar girdle but have reduced it by losing the clavicle and rendering the other structures partly vestigial.

Mammals

The mammalian girdle is much reduced except in the monotremes, which retain the reptilian type. In *Ornithorhynchus* (Fig. 151) a large

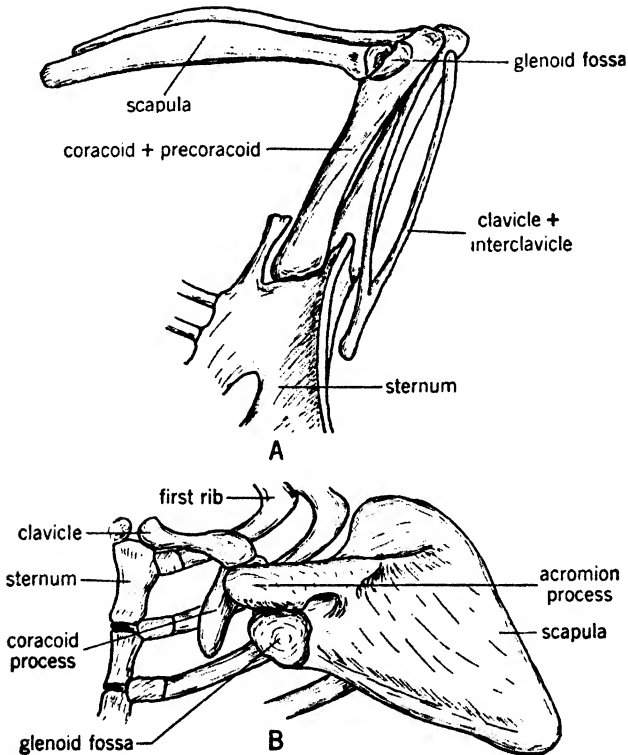


FIG. 159. A, Pectoral girdle of domestic turkey; B, Pectoral girdle of gorilla.

interclavicle, or episternum, forms the connection with the sternum; the coracoid is attached to the scapula; a small precoracoid is present; and a clavicle completes the girdle. Marsupials and placentals retain only the scapula and clavicle. The coracoid is vestigial and fuses with the scapula forming a small coracoid process (Fig. 159 B). This process is considered by Romer (1945) as a precoracoid. The clavicle ties the girdle together and is a useful element for those animals that pull with their forelegs. It is retained in those mammals that climb or have had a comparatively recent arboreal ancestry. It is absent in many ungulates, where it appears only in the embryo. The clavicle

is present in some carnivores, such as the cat, as a reduced and unattached bone embedded in the muscles. The tying of the scapula to the sternum is very important in any mammal that is able to hold its weight by its anterior limbs. The scapula consists of a flat blade, generally with a longitudinal spine, ending in an acromion process. It terminates ventrally in a cavity, the glenoid fossa, for the articulation of the humerus. A coracoid process, all that remains of the coracoid bone, projects from the anterior rim of the glenoid fossa. A

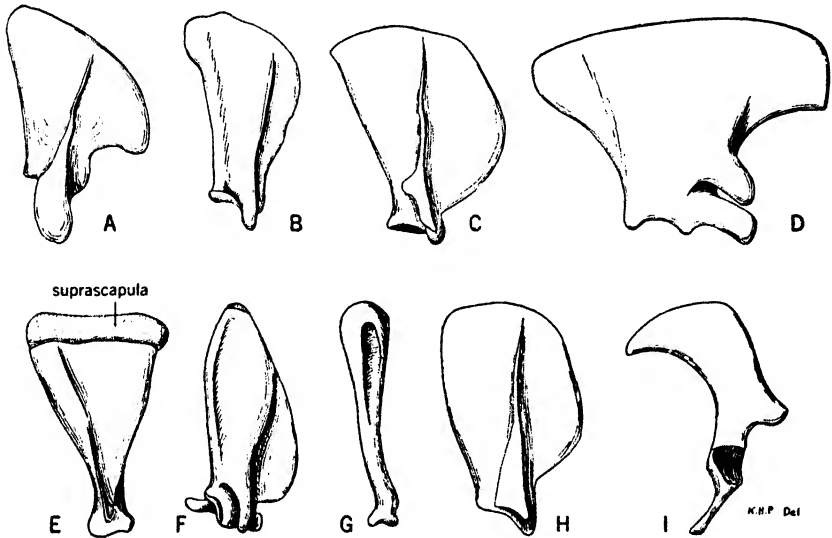


FIG. 160. Scapulae of mammals. A, gorilla; B, monkey; C, mountain lion; D, dolphin; E, deer; F, bat; G, mole; H, opossum; I, duckbill (monotreme).

cartilaginous suprascapula (Fig. 160) lengthens the blade on its dorsal border. The scapulae of the different groups are quite characteristic, and it is evident that their shape depends on the work they do. Scapulae may be long and have a small spine, as in the ungulates; extremely elongated, as in insectivores; rounded, as in the carnivores; or rounded and flat with no spine, as in the porpoises. A long acromion process is generally associated with climbing (Fig. 160).

Pelvic or Posterior Girdle

The pelvis, or posterior girdle (Fig. 161), serves two main functions: first, to supply a solid articulation for the femur; and second, to supply insertions and origins for the many muscles connected with the posterior limbs. It differs from the pectoral girdle in that it is always deep in the tissues and has never had any additions from dermal sources. Above the fishes, it is always attached to the vertebral column

by modified sacral ribs, lightly in the Amphibia, with a gradual improvement of the articulation through to the mammals. Each half consists of three elements, the ilium, pubis, and ischium. All three of these elements meet and take part in the formation of the acetabulum or socket for the articulation of the femur. The ilium, or dorsal element, which always articulates with the sacral elements, is variable in shape. It is usually a straight bar but is T-shaped in birds and ornithischian dinosaurs. The pubis, or ventral element, extends anteriorly except in birds, and it may join its fellow of the other side to form a ventral arch.

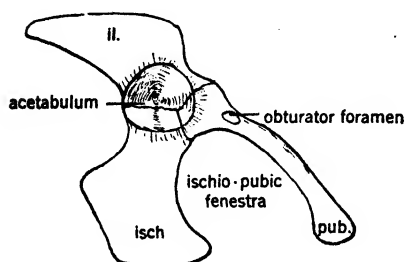


FIG. 161. Right pelvic girdle of *Sceloporus*.

The obturator nerve generally extends through a large foramen in the pubis. The distal ends of the pubis and ischium may be joined, as in some of the birds and reptiles. Some reptiles, monotremes, and marsupials have epipubics. The ischium, or posterior ventral element, is generally large, and it may join its fellow of the other side to form an arch. The acetabulum,

or the socket, with which the head of the femur articulates, is formed by the bones of the pelvic girdle. Sometimes an acetabular (cotyloid) bone (Fig. 163) is formed as a separate ossification.

Fishes

The pelvic girdle of the elasmobranchs (Fig. 162) is a bar of cartilage that extends across the body between the fins and appears to have been a part of the fin-base.

Crossopterygians develop a pair of bony bars, and the teleosts have the same type of structure, which seems to be a part of the fin-base extending into the body wall.

Amphibians

Typical pelvic structures first appear in the amphibians, and they may be correlated strictly with tetrapods and land life. The connection between the ilium and the vertebral column is made first in the amphibians. It appears to be a new articulation in *Necturus* (Fig. 162 B), for it is very variable, and its position on the column may shift forward or backward. Each half of the girdle of *Necturus* consists of an ilium, an ischium, and a large ventral cartilage from which the pubis may ossify. Much of the girdle remains undifferentiated cartilage in the urodeles. The Anura have a completely ossified girdle

with three bones well developed and meeting in an acetabulum. The high development found in the Anura is correlated with the jumping habits of this group.

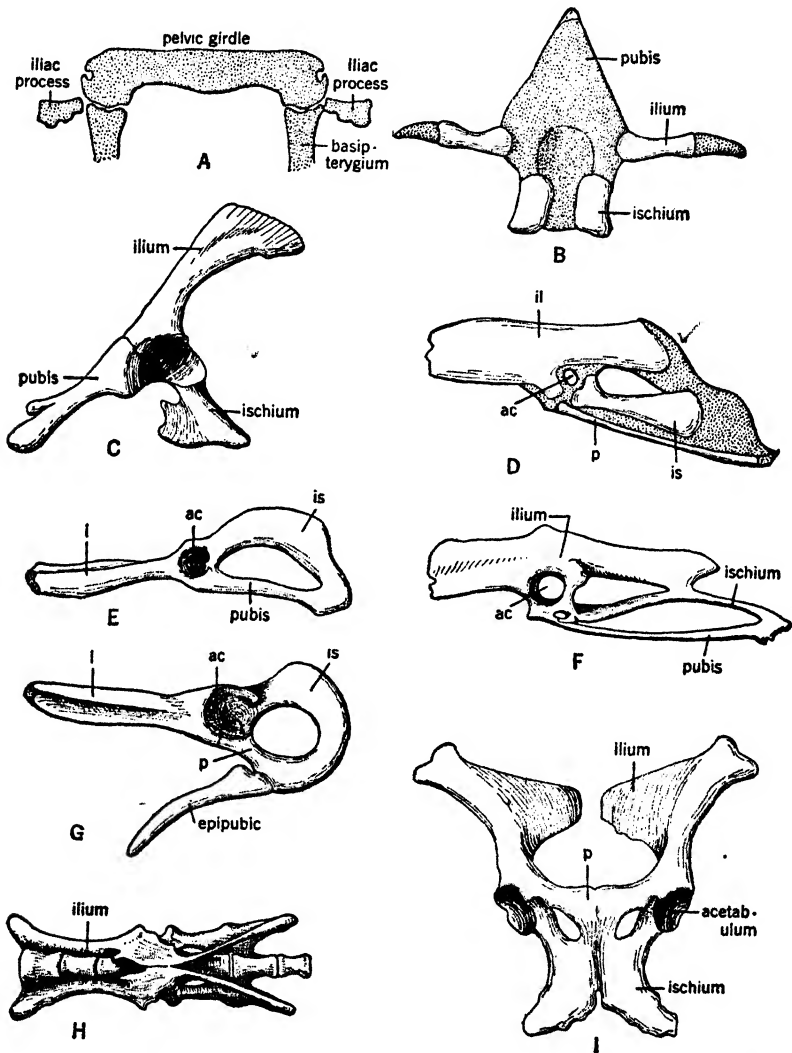


FIG. 162. Types of pelvic girdles. A, shark (*Squalus*); B, mud puppy (*Necturus*); C, turtle (*Chelydra*); D, chicken (*Gallus*); E, muskrat (*Odonatra*); F, rhea; G, opossum (*Didelphis*); H, mole (*Scalops*); I, horse (*Equus*).

Reptiles

The reptiles (Fig. 162 C) show much variation of the pelvis, owing to different walking adaptations. Generally the girdle is very solid and substantial, its structure showing close correlation with the needs of

land life. The attachment to the vertebral column is through one or more specialized sacral vertebrae, generally two in modern forms, but in the highly specialized reptiles such as *Trachodon* there were eight or nine. The pelvis is always triradiate (Fig. 162 C) and generally has a large opening between the pubis and the ischium. Usually all three bones take a part in forming the acetabulum, the socket which supplies the articulation for the head of the femur. Reptiles sometimes develop a pair of epipubic bones extending forward from the pubis.

Birds

In birds the pelvis is also a highly specialized structure, adapted to bipedal habits (Fig. 162). The ilium is greatly elongated and attached to the synsacrum (sacrum fused with caudal and trunk vertebrae). Except in ratites there is no ventral fusion between the two sides. The ischium and pubis of adults are directed posteriorly—a secondary condition, since in the embryo they are like those of the reptiles. The pubis is a long slender bone extending posteriorly and parallel to the ischium. Both are free posteriorly. A small prepubic process occurs just anterior to the acetabulum. All three bones contribute to the formation of the acetabulum which is perforated by the acetabular foramen.

Mammals

In mammals the three elements of the posterior girdle tend to fuse into one piece (innominate bone), so that the separate bones are not distinct in adults, but the triradiate structure is retained. The pubis, ischium, and ilium meet in the acetabulum. At the point of union, a small triangular bone, the cotyloid or acetabular bone appears in the embryo (Fig. 163) and in some very young mammals. This bone becomes fused with the other elements in the adult. The ilium can always be recognized as the bone articulating with the sacrum.

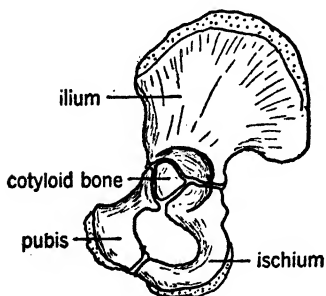


FIG. 163. Left innominate bone of human fetus at six months.

The shape of the ilium (Fig. 162) varies with the habits; it is generally long in running animals; wide and extending out laterally in heavy, peg-legged animals, such as the rhinoceros and the elephant; round in apes and man; and vestigial in whales and sea-cows. The pubics form the anteroventral element and are fused anteriorly. A pair of epipubics extends anteriorly from the pubics in the monotremes and marsupials but are absent in adult placentals, although

sometimes present in the embryos. The ischium forms the postero-ventral element and can be easily remembered as the bone we sit on. Both the ischium and the pubis unite ventrally in a symphysis. The obturator foramen is the space formed by the ventral union of the pubis and the ischium. In man the pelvis is called the innominate bone.

Fins

Fishes develop two types of fins, median and paired, which have similar structure although they are quite unrelated. The median fins of fishes are somewhat varied and may consist of a continuous finfold, or they may be separate fins. Early in the history of fishes these fins developed supporting structures of several types. The generally accepted theory of fin formation is that originally the fin was formed

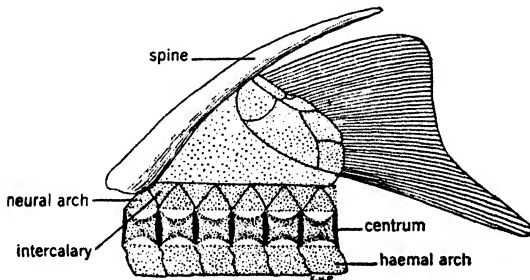


FIG. 164. Median dorsal fin and part of vertebral column of *Squalus acanthias*.

over a number of somites with a supporting structure consisting of a chondral pterygiophore extending out from each segment. These pterygiophores became broken into several elements, the proximals known as basalia and the distals known as radialia and terminated by dermal rays. The basals of the paired fins grew together and became attached from their original somites except at one point which formed the base of the fin. The distal part of the fins is usually supported by a number of slender fin rays of several types. The girdle was formed by the inward growth of a basal from each fin.

Median Fins

The median fins may be built up entirely of connective tissue and skin, or they may have supports of different kinds. Placoderms had spines and curious elements along the median line of the back which may be interpreted as median appendages. The elasmobranchs have cartilaginous supports consisting of basalia, which come in contact with vertebrae, and a radial series in the fin itself. The distal part is

supported by flexible unjointed rays of a fibrous material which also occurs in the Holocephali. Remnants of these rays appear in the development of the bony fishes and occur in a few adults. In teleosts the skeletal part of the median fin becomes more complex (Fig. 165). The

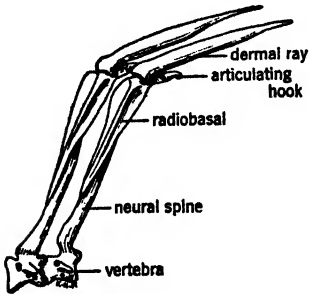


FIG. 165. Bony elements attaching median fin to axial skeleton in a perch.

neural spines are grooved on the anterior side to form an articulation with the radiobasals and thus build up a good mechanical structure in combination with the dermal supports. The rays are branched, jointed bony structures shown by Goodrich to be homologous to scales.

Median folds or fins appear in young amphibians and in all urodeles that remain permanently in the water. The median fins that develop in ichthyosaurs, and those found in water mammals such as whales and dolphins, consist of adipose tissue and are practically without supporting structures. These fins are not homologous to those of fishes.

Caudal Fin

The caudal or tail fin is the main propelling device in most aquatic animals and has many modifications. The caudal fin of fishes was originally a part of the median fold which extended around the body, as in the cyclostomes. Primitively, it was without supports and therefore of little use as a propeller. The shape was rounded or pointed, at first, with the blades equal and the axis in the middle. This diphyccercal tail (Fig. 166) is found in cyclostomes, dipnoans, crossopterygians, primitive sharks, and many deep-sea teleosts. The heterocercal type (Fig. 166), found in modern sharks, sturgeons, paddlefish, and other forms, is two-lobed with the main axis extending into the dorsal lobe, whereas the ventral lobe is smaller and formed by fleshy tissue. The homocercal tail fin (Fig. 166), found in most teleosts, is derived from a heterocercal type in which the vertebral column does not extend very far into the dorsal lobe, and the lower lobe is developed so that it is equal to the dorsal, thus forming a symmetrical structure (Fig. 166). The gephyrocercal tail (Fig. 166) of the gars and *Amia* is really a modified heterocercal structure in which the tail appears to be symmetrical but retains the asymmetrical supporting structures. These have a heterocercal tail when first hatched, but they tend to lose the dorsal lobe, retaining the rounded ventral lobe, with the vertebral column extending into it, as the adult tail.

Paired Fins

Paired fins are found throughout most of the fish group above the Agnatha. At first mere lappets (Fig. 155), as in *Cladoselache*, a primitive shark, the paired fins developed radials, horny rays, and

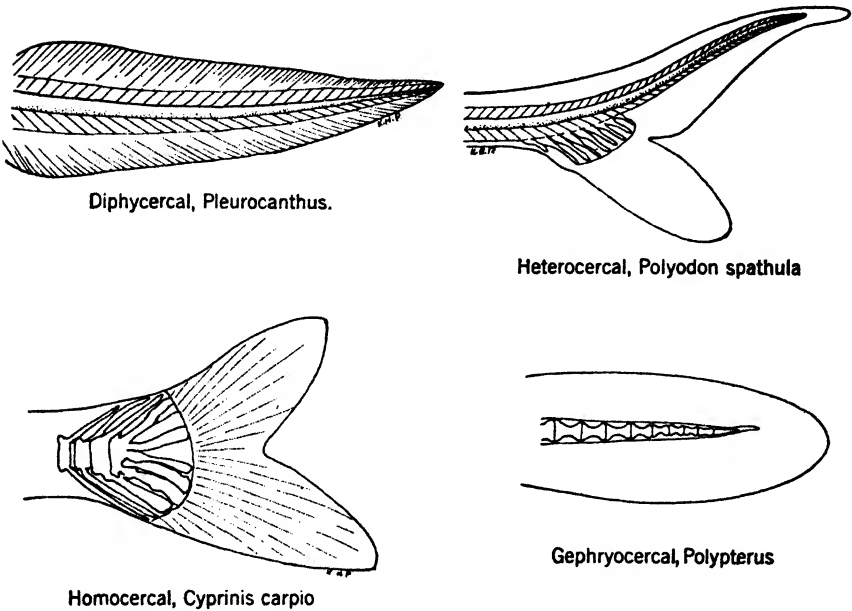


FIG. 166. Types of fish tails.

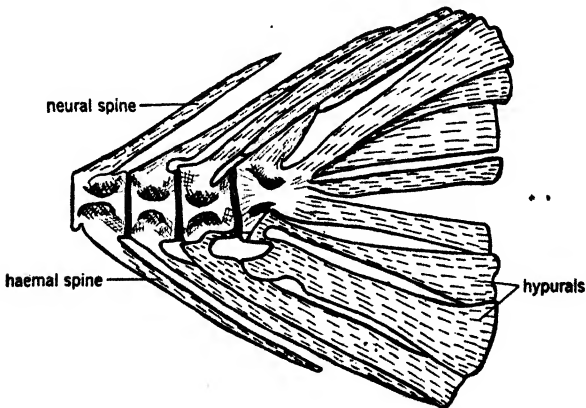


FIG. 167. Bony structure at base of caudal fin of a catfish.

the mesodermal scales that are fused to form the rays of the bony fishes. The paired lappets of *Cladoselache* served only as keels (Fig. 155), but in their structure the framework for the future skeleton

of the fin was being laid down. The paired fins of the elasmobranchs are rather clumsy structures in the older forms but better organized in recent types. The supports of the paired fins consist of two semi-circular bars, the pectoral and pelvic girdles, to each of which a series of cartilages is attached to form the base of the fins. These cartilages normally consist of a propterygium, a mesopterygium, and a metapterygium (Fig. 156). The propterygium articulates with the girdle; the others form the axis of the fin. To these three cartilages are attached a number of radials, beyond which are the rays, forming the rest of the fin.

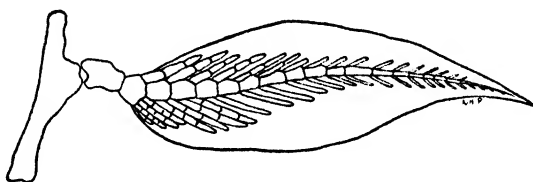


FIG. 168. Pectoral fin of lungfish, *Ceratodus*, showing the biserial arrangement of the fin elements. After Gregory and Raven.

The Dipnoi (lungfishes) developed a biserial fin, with a median axis, a condition rare in the fish series. This type of fin was used by Gegenbauer to develop his theory of the origin of fins from gill arches.

The pectoral fins of *Polypterus* are extruded by the elongation of the basal parts, so that they have the appearance of limbs and somewhat resemble the lobed fins of the crossopterygians. In teleosts the basal elements of the fins are reduced or absent, and a few of the radials form the foundation, the rest being supported by a large number of fin rays of dermal origin. The paired fins, normally found in the pectoral and pelvic regions, may shift so that the pelvic pair is anterior to the pectoral pair.

Paired Limbs

The transition from a fin to a tetrapod limb was one of the most important changes that had to occur before the fish ancestor of the tetrapod was able to move about on land. This change occurred in the crossopterygians which developed the bones (basalia and radialia) of their paired fins into elongated structures which resembled very closely the bones of the appendages of the early amphibian *Eryops*. Unfortunately only the fin structures of several crossopterygians, *Eusthenopteron* and *Sauripterus* (Figs. 169, 170), are well known. The bones of their paired fins show an arrangement similar to that of the tetrapod limb, and some homologies can be traced. These crossop-

terygians were probably able to use these appendages for a sort of crawling movement rather than for the balancing-swimming movements of most fishes.

The elongated biserial fin of the Dipnoi (Fig. 168), in which there is a main axis with a series of pre- and postaxial radials, led Gegenbauer to consider them as ancestral to the tetrapod limbs but his view was later abandoned in favor of the crossopterygians. Holmgren (1933, 1939) has more recently concluded from embryological studies that the limbs of urodeles are derived from dipnoian paired fins, and, if true, this would indicate a separate origin for the urodeles. The paleontological evidence supports the crossopterygian origin.

The first tetrapod appendages, being at right angles to the body, were not in a position to support its weight. For this reason amphibians and the early reptiles could not sustain the body for any great length of time. With further adaption the legs of higher reptiles and mammals shifted under the body so that there was a better distribution of the weight and a better mechanical adjustment.

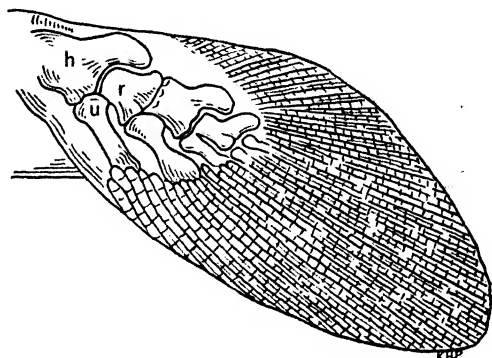


FIG. 169. Left pectoral fin of crossopterygian, *Eusthenopteron* showing the fin elements and their suggested homology. After Gregory and Raven.

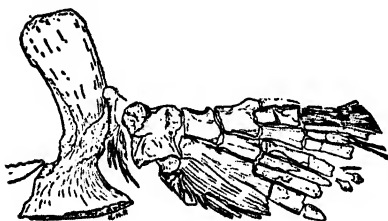


FIG. 170. [Pectoral girdle and paddle of crossopterygian, *Sauripterus taylori*, showing fin elements. After Gregory and Raven.

The pattern of the tetrapod limb is surprisingly regular and persistent. The anterior and posterior limbs are made on the same plan, with corresponding elements and a similar musculature.

Tetrapods developed typically a five-toe or pentadactyl plan for each foot. There is some evidence that some early tetrapods had as many as seven toes, although some early amphibians had only three toes. Modern tetrapods have adhered to the pentadactyl plan, some modifying the foot by losing toes.

The limbs of tetrapods are highly specialized and closely correlated with life habits. The most primitive type of the foot appears to be the plantigrade, in which the whole under surface is used in walking;

a modification, the digitigrade, elevates the posterior part of the foot so that the tarsal or carpal segments do not come in contact with the ground, whereas the unguligrade, the most extreme type, walks entirely upon the ends of the fingers or toes, which are encased in a horny hoof.

Segments of the Limbs

The limbs of tetrapods may be said to be composed of three segments. The first segment consists of the proximal part of the limb extending to the elbow or the knee. The second segment is that part extending from the elbow or the knee to the wrist or ankle. The third segment is composed of the foot or hand and the wrist or the ankle.

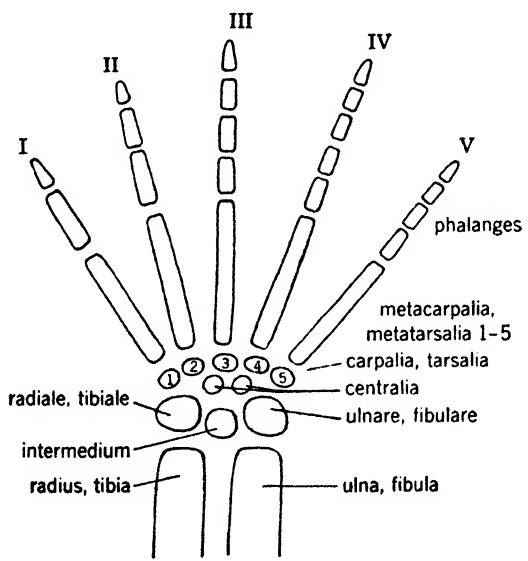


FIG. 171. Diagram of tetrapod foot.

The segments of the anterior and posterior limbs, being made up of similar parts, may be compared as follows:

Segment	Anterior limb	Posterior limb
First	Humerus (upper arm)	Femur (thigh)
Second	<div><div>Radius</div><div>Ulna</div></div> (forearm)	<div><div>Tibia</div><div>Fibula</div></div> (shank)
Third	<div><div>Carpus (wrist)</div><div>Metacarpus (hand)</div><div>Phalanges (fingers)</div></div>	<div><div>Tarsus (ankle)</div><div>Metatarsus (foot)</div><div>Phalanges (toes)</div></div>

The plan for the third segment is identical for fore and hind limb. The bones of the ankle (tarsus) and the wrist (carpus) are collectively known respectively as tarsals and carpals. Each fundamentally follows the same plan (Fig. 171), although no living vertebrate adheres

strictly to this arrangement. In the higher vertebrates, additional bones are often found in the carpus and the tarsus. These are sesamoid bones and are formed from ossifications in the tendons. In man and in certain other mammals, some of the sesamoid bones of the carpus are called pisiform bones. The bones of each limb are described in the following sections.

Anterior Limbs

The first segment of the anterior limb is formed by the humerus (Fig. 174), a single element, which articulates proximally with the

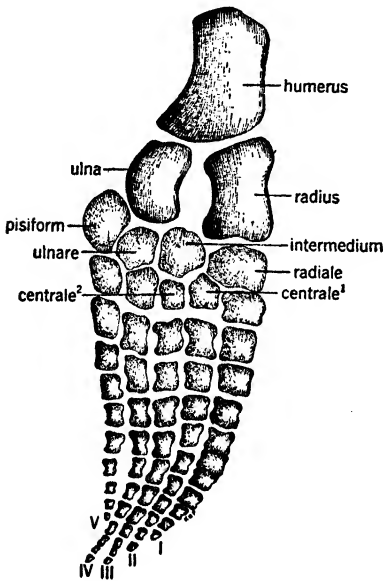


FIG. 172. Paddle of a water reptile (*Ichthyosaurus*). After Abel.

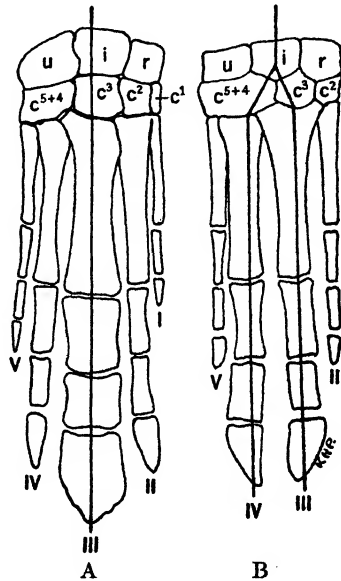


FIG. 173. Diagram showing the right hand of perissodactyl (A), and artiodactyl (B). A, mesaxonic; B, paraxonic. After Weber.

glenoid fossa of the scapula and distally with the radius and ulna. Its shape varies with its use in different adaptations. It has an articular head at the proximal end, a shaft, and a trochlear surface distally for the articulation with the radius and ulna. Several tuberosities for muscular insertion develop at the anterior end, and lateral foramina, the ectepicondylar and entepicondylar, may be present at the distal end.

The forearm (Fig. 175), or second segment, consists of two bones, the radius and ulna. In lower forms these bones are much alike, but in

the higher, especially mammals, the ability to twist (pronation and supination) becomes highly developed with corresponding changes in the two bones. In animals specialized for running, the two bones are joined, making the segment stronger.

The carpus consists of a varying number of small elements that connect with the radius and ulna proximally, and with the metacarpus distally. Originally the carpals were in three rows, but in modern forms the middle row is absent or consists of but one or two small

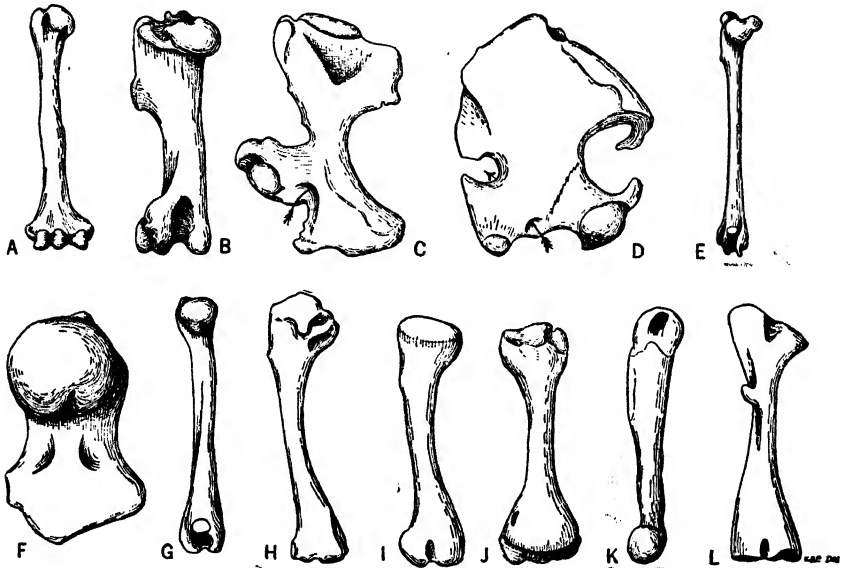


FIG. 174. A series of humeri (left) drawn to the same size to show variations in the different vertebrate classes. A, gorilla; B, horse; C, spiny anteater (*Echidna*); D, mole (*Scalops*); E, rabbit (*Lepus*); F, dolphin; G, cat; H, chicken (*Gallus*); I, alligator; J, Gila Monster (*Heloderma*); K, frog (*Rana*); L, salamander (*Ambystoma*).

bones, called centralia. The proximal row consists of three bones, an ulnare at the end of the ulna, a radiale at the end of the radius, and an intermedium between. The third or distal row consists typically of five carpalia.

The greatest change in the carpals comes in the modification necessary to form the mesaxonic and paraxonic (Fig. 173) types of hands and feet. The main axis of stress goes through the third digit in the mesaxonic type, and between the third and fourth digits in the paraxonic type.

The metacarpus consists of a series of elongated bones that form the body of the hand. They articulate distally with the digits and usually equal them in number. Proximally the metacarpals articulate with

THE BONES OF THE CARPUS, WITH SYNONYMS

	<i>Terms used in comparative anatomy</i>	<i>Abbreviations</i>	<i>Terms used in medical anatomy</i>	<i>Synonyms</i>
Proximal row	Radiale	r	Scaphoid	Navicular
	Intermedium	i	Semilunar	Lunate
	Ulnare	u	Triquetral	Cuneiform, pyramidal
	Sesamoid	p	Pisiform	
Medial row	Centrale (0 — 3)	Cen.		
	Carpale 1	c ¹	Trapezium	Multangular major
Distal row	Carpale 2	c ²	Trapezoid	Multangular minor
	Carpale 3	c ³	Capitate	Magnum
	Carpale 4	c ⁴	Hamate	Uncinate, unciform
	Carpale 5	c ⁵		

the row of carpals named carpalia. Primitively the number of carpalia is the same as that of the metacarpals, but there is a tendency for a fusion of the carpalia especially in carpalia 4 and 5 (Figs. 176, 177, 179, 180).

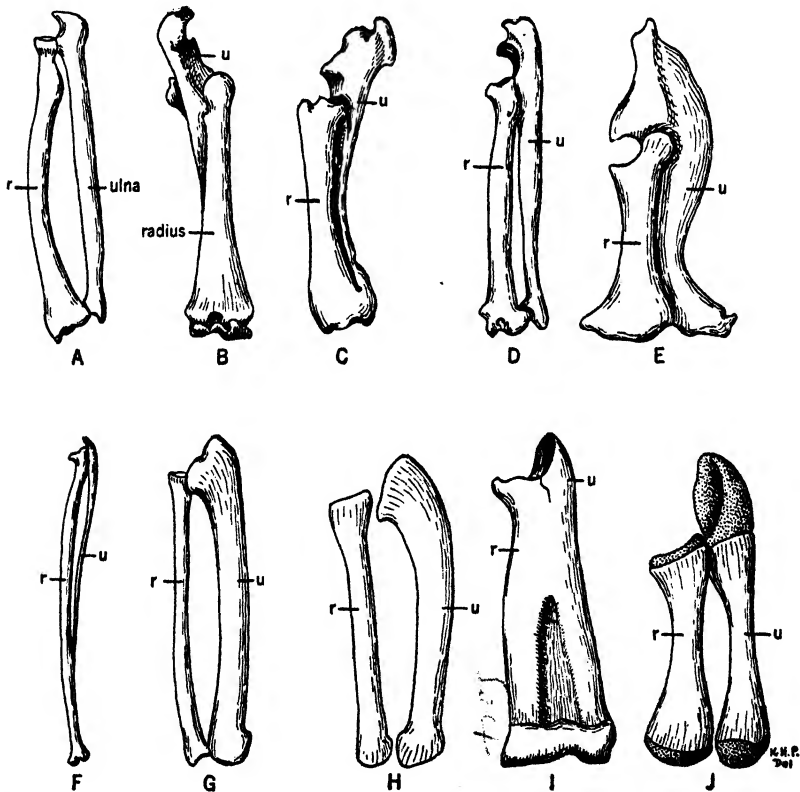


FIG. 175. Series of bones of the forearm to show variations of radius and ulna in different vertebrate classes. A, ape (*Orang*); B, horse (*Equus*); C, cow (*Bos*); D, cat (*Felis*); E, mole (*Scalops*); F, bat (*Pteropus*); G, turkey (*Meleagris*); H, alligator; I, frog (*Rana*); J, mud puppy (*Necturus*).

Amphibians

The plan of the fore limb (Fig. 176) consists of the following parts: a single proximal element, the humerus; a forearm composed of a radius and ulna; and the distal segment composed of a carpal series, the metacarpals and the digits, which are usually reduced to four. The long bones usually show less differentiation and development than in the higher vertebrates. The carpals are frequently reduced and imperfectly formed. Those of *Necturus* are represented by three rows

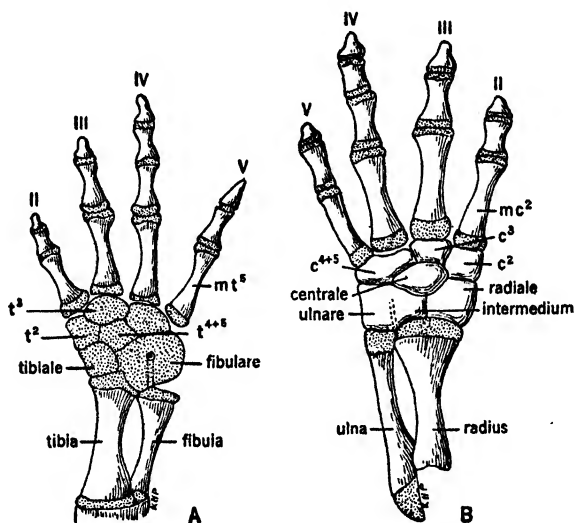


FIG. 176. A, foot of *Necturus*; B, hand of *Necturus*.

of small partially ossified bones (Fig. 176) which are rather difficult to make out. The frog has a much better-developed set of carpals. The proximal row contains an ulnare and a radiale with a centrale on the inner side of the radiale. Three carpalia are present at the base of the metacarpals. The outer carpal is large and consists of the fusion of carpalia III, IV, and V. *Ambystoma* has a carpal series of three rows: the ulnare, intermedium and radiale; a mediale centrale; and a distal row of carpalia I, II, III, and IV articulating with the metacarpals.

Reptiles

The fore limb of those reptiles which have not lost their limbs (Ophidia) or modified their limbs for flying (Pterodactyls) or for an aquatic life (Ichthyosaurs) has the usual elements well developed. The humerus has a distinct head for articulation with the glenoid

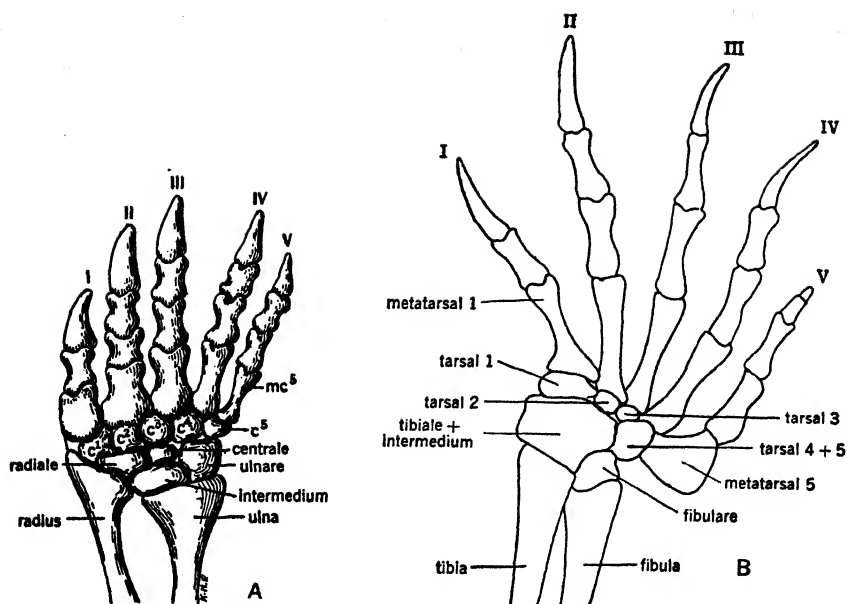


FIG. 177. A, right manus of turtle; B, right pes of turtle, *Pseudemys troosti*.

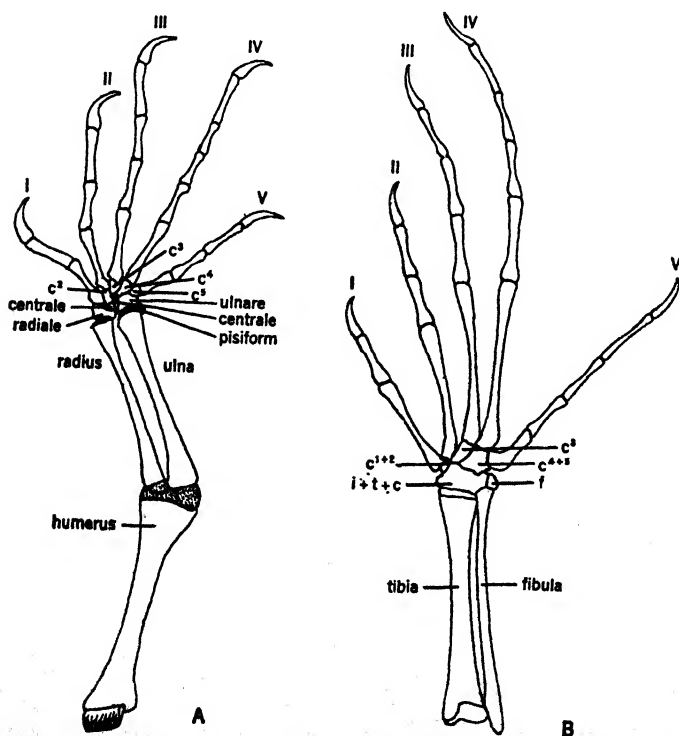


FIG. 178. A, right manus, B, right pes of *Sceloporus*.

fossa of the scapula. The radius and ulna are quite similar and do not show as great differentiation as found in the mammals. The carpals tend to adhere to the primitive plan. The turtle has an ulnare and intermedium in the proximal row. A long bone composed of a fused radiale and one or more centralia forms the second row. The third row is composed of five carpalia. The carpus of *Sphenodon* consists of an outer sesamoid bone, an ulnare, a large intermedium, and a radiale in the first row. The second row consists of two centralia and the distal row of five carpalia. The lizard *Sceloporus* (Fig. 178) has a proximal row consisting of a radiale, two centralia, an ulnare, and a sesamoid bone. Four carpalia complete the next row, the first carpale apparently being absent. The number of phalanges for the third, fourth, and fifth digits ranges from four to five.

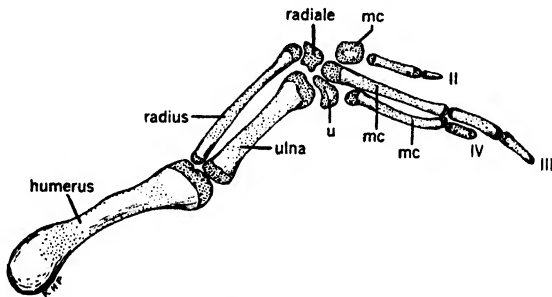


FIG. 179. Right wing of a chicken, just hatched.

Birds

The anterior limb of a bird (Fig. 179) is modified for flight by numerous changes in the carpus and hand. The humerus is of the usual bird form, the radius and the ulna slightly specialized, the ulna having the flight feathers attached to its posterior border. The bones of the carpus are more specialized, the radiale and the ulnare remaining free, while the distal row of carpals joins with the metacarpals to form the carpometacarpus. These metacarpals are considered as parts of the second, third, and fourth digits. Digit 2 has a short metacarpal and one phalanx, digit 3 a large metacarpal and two phalanges, and digit 4 one long metacarpal and one phalanx. In birds generally, there is not much variation in the manus, since it is so closely correlated with the type of flight and the rapidity of the movement of the wings. Running birds have a much reduced anterior limb.

Mammals

The proximal segment of the fore limb of all mammals has a single bone, the humerus. Its proximal end has a large head which

articulates with the glenoid cavity, a greater tuberosity which is continued down the length of the shaft as the deltoid ridge, and a lesser tuberosity that is mesial on the head. The groove for the tendon of the biceps is between the two tuberosities. The distal end is developed into a trochlea for the articulation of the radius and ulna. The posterior face of this distal end has a deep fossa for the olecranon process of the ulna.

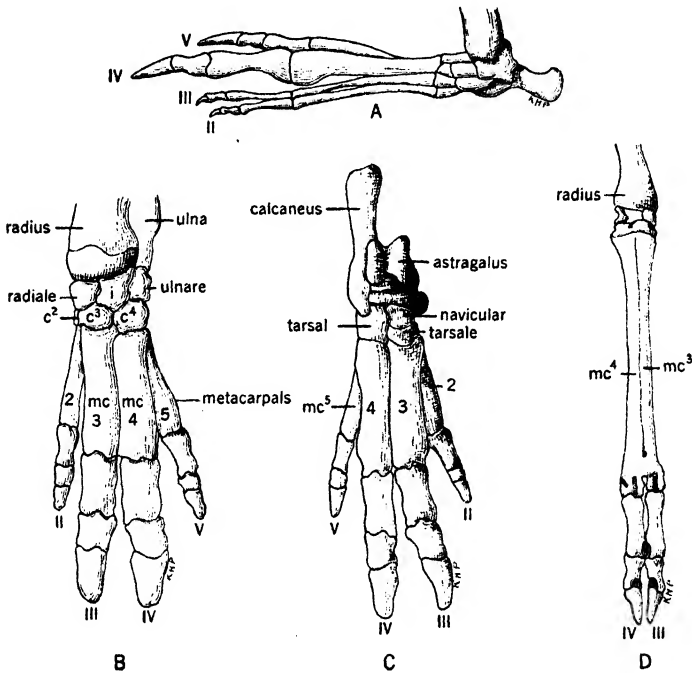


FIG. 180. Feet of mammals. *A*, right pes of a kangaroo, *Dorcopsis* (after Abel); *B*, left manus of pig (after Sisson); *C*, right pes of pig (after Sisson); *D*, right manus of antelope.

The ulna is post axial, articulating with the humerus by a deep sigmoid notch, which is followed by the olecranon process. It has a small notch distal to the sigmoid for the articulation with the head of the radius. It articulates with the carpus through the ulnare, or triquetral. The radius is preaxial, rod-like, and decidedly curved. Proximally, it articulates with the humerus and ulna, and distally with the radiale. Through its articulations and musculature the radius of some mammals is able to perform a twisting movement. (Figs. 174, 175.) Cetacea and Sirenia have short and more or less undifferentiated long bones. Ungulates have reduced the ulna and enlarged the radius, often fusing them.

The mammals often modify the carpals by fusing some of them. The human carpus (Fig. 182) contains a proximal row of four bones: the radiale (scaphoid), the intermedium (semilunar), the ulnare (triquetral), and a sesamoid bone (pisiform). The remaining row consists of four bones representing the carpalia in their normal sequence except that the outer bone (hamate) consists of fused fourth and fifth carpalia. The rat has the same arrangement except that a centrale is present, wedged between the intermedium and the distal row, representing the middle row absent in many mammals. (Figs. 180, 181, 182.)

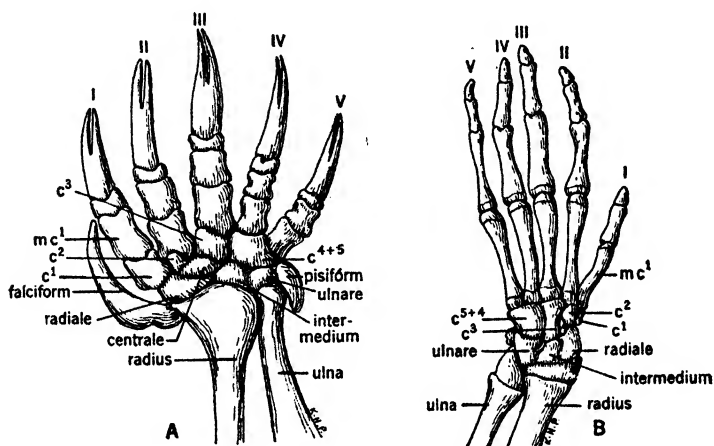


FIG. 181. Mammalian hands. *A*, right manus of mole (after Weber); *B*, left manus of monkey (*Macacus rhesus*).

The cat has a small sesamoid bone, a large fused intermedium and radiale (scapholunar), and an ulnare (triquetral) in the proximal row. The distal row like that of the human has four bones representing the carpalia in their normal sequence with the hamate formed of the fused fourth and fifth carpalia. A sesamoid bone is on the outer margin.

In ungulates considerable modification has occurred, especially in the horse, where only one functional digit is retained. Only the radius articulates with the carpus. The carpales consist of a radiale (scaphoid), an intermedium (lunar), an ulnare (cuneiform), and a small outer pisiform bone. The distal row contains the second carpale (trapezoid), a broad flat third carpale (magnum), and a small fused fourth and fifth carpalia (hamate). The third metacarpal forms the long shank below, ending in three short phalanges. Vestigial second and fourth metacarpalia are present as splints on the lateral margins of the third metacarpal.

Ruminants have two well-developed digits with the corresponding

metacarpalia fused together. Two additional digits are present but are represented by vestigial digits and metacarpalia.

In Cetacea it is difficult to homologize the carpalia as they are often imperfectly ossified. The phalanges are very flat. Cetacea have diverged from the mammalian formula of three phalanges and may have as many as twelve phalanges on one digit.

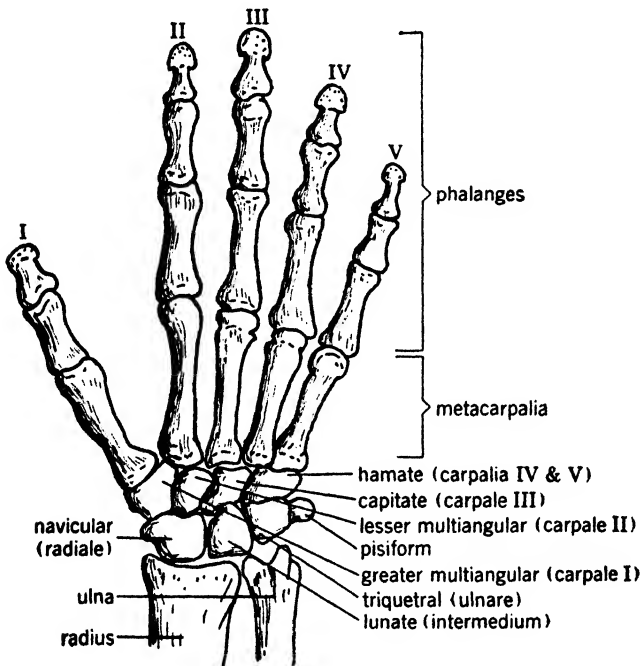


FIG. 182. Bones of human hand.

Posterior Limbs

The posterior or hind limb is generally much heavier than the anterior and receives more of the stress and strain in running and jumping. The first segment of the hind limb is composed of the femur (Fig. 183), which is usually rather heavy and elongated and articulates with the acetabulum of the pelvis. In higher vertebrates there is a tendency to develop the head medially, often with a neck. Trochanters and muscle insertions may develop on the head and shaft. Articulation with the tibia and fibula is by a horseshoe-shaped surface, and the patella, a sesamoid bone, slides over this articulation.

The second segment (Fig. 184) of the posterior limb consists of the tibia and fibula, the tibia corresponding in position to the radius, and the fibula to the ulna. The tibia tends to bear most of the weight

in the higher vertebrates. The fibula is variable and may become greatly modified or even vestigial.

The third segment contains the tarsus, which corresponds to the carpus and is made up of a similar arrangement of three rows of small tarsals. Coupled with the variable use of the foot, there is

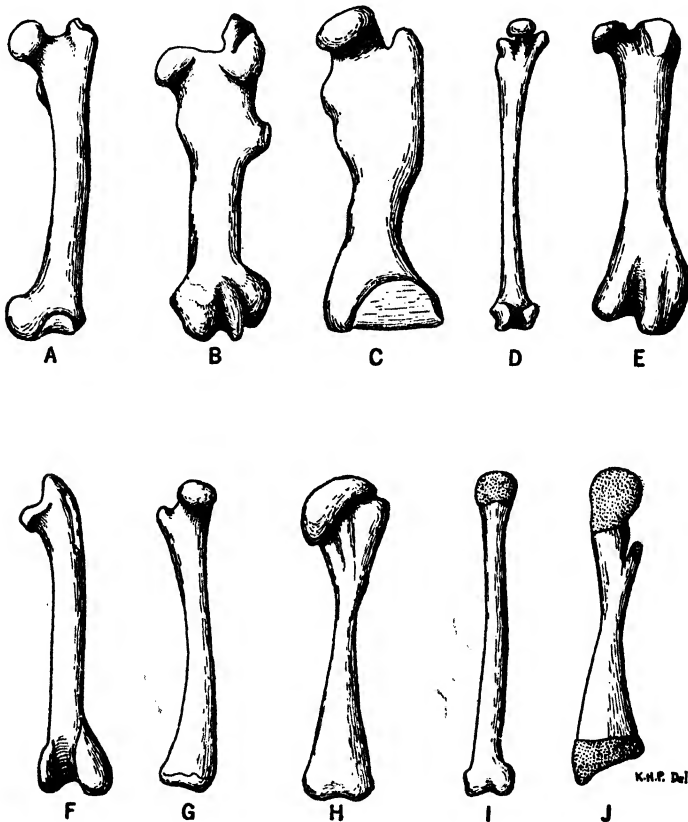


FIG. 183. Series of femurs showing variations in vertebrate classes. A, ape (*Orang*); B, horse (*Equus*); C, spiny anteater (*Echidna*); D, bat (*Pteropus*); E, pelican (*Pelicanus*); F, chicken (*Gallus*); G, horned lizard (*Phrynosoma*); H, turtle (*Chelydra*); I, frog (*Rana*); J, mud puppy (*Necturus*).

much modification of these bones, such as shifting in position and joining with other elements or dropping out entirely. The original plan of the tarsus shows the following arrangement. The proximal row of tarsals contains the fibulare at the end of the fibula, the ulnare at the end of the ulna, and an intermedium between. Several centralia originally formed the second row. The third row contains the tarsalia, of which there were originally five.

THE BONES OF THE TARSUS, WITH SYNONYMS

	Terms used in comparative anatomy	Abbreviations	Terms used in medical anatomy
Proximal row	{ Fibulare Intermedium Tibiale	f i t	Calcaneus Talus or astragalus (the same as tibiale + intermedium or intermedium + centrale)
Medial row	Centrale	Cen.	Navicular
	{ Tarsale 1 Tarsale 2 Tarsale 3 Tarsale 4 Tarsale 5 }	t ¹ t ² t ³ t ⁴ t ⁵	Entocuneiform Mesocuneiform Ectocuneiform
Distal row			Cuboid

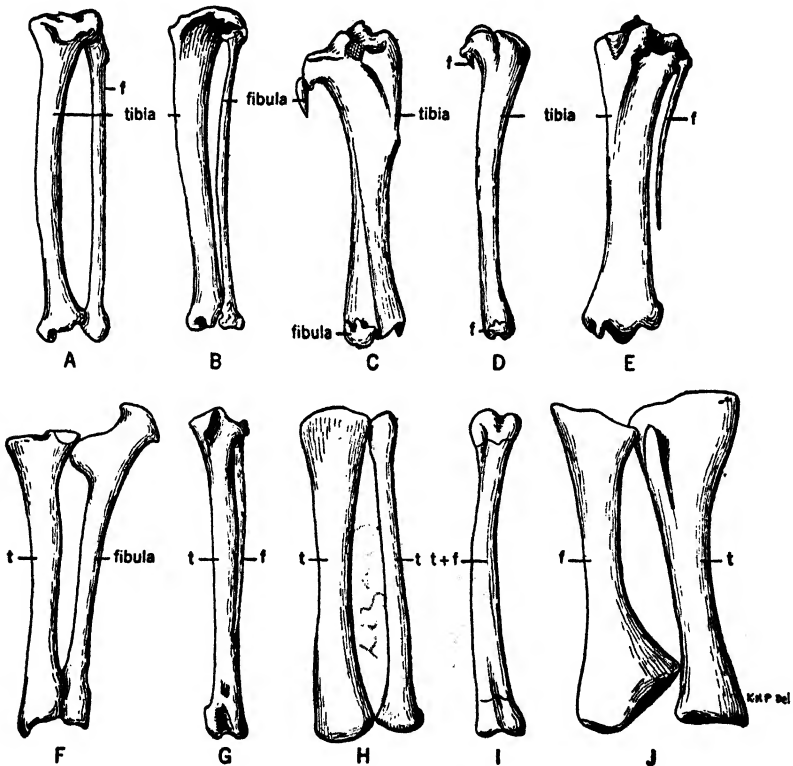


FIG. 184. Tibia and fibula in different vertebrate classes, reduced to the same size. A, ape (*Orang*); B, cat (*Felis*); C, cow (*Bos*); D, Antelope (*Antilocapra*); E, horse (*Equus*); F, Manis; G, turkey (*Meleagris*); H, alligator; I, frog (*Rana*); J, mud puppy (*Necturus*).

The metatarsal bones are elongated elements. They form the articulation for the digits distally and usually equal the number of digits. They articulate with the tarsus, and, although primitively there was

a tarsal bone for each metatarsal, in most animals the tarsalia are reduced either by fusion or by elimination.

Each digit is made up of a series of phalangeal bones that vary in

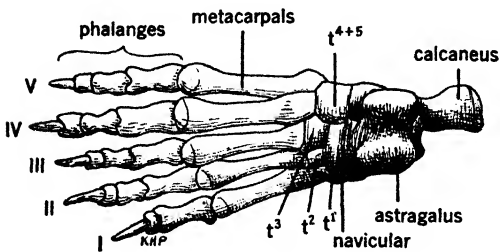


FIG. 185. Right pes of a bear showing arrangement of tarsals and digits.

number but are usually quite regular within the classes. The digits are designated as digits I, II, III, etc. The phalangeal formula becomes quite an aid in classification. The table gives the phalangeal formula for the manus and pes of a few representative tetrapods. The formula is made up of five terms, referring to the five digits (beginning with the first digit, i.e., the thumb or great toe), and the number of phalanges in each digit is indicated by the numeral. Missing digits are indicated by zero.

PHALANGEAL FORMULA IN REPRESENTATIVE VERTEBRATES

	Manus	Pes
Salamander, <i>Cryptobranchus</i>	0-2-2-3-2	2-2-3-3-2
Bullfrog, <i>Rana catesbiana</i>	0-2-2-3-3	2-2-3-4-3
Turtle, <i>Chelydra serpentina</i>	2-3-3-3-3	2-3-3-3-3
Alligator, <i>Alligator</i>	2-3-4-3-3	2-3-4-3-0
Tuatera, <i>Sphenodon</i>	2-3-4-5-3	2-3-4-5-4
Chicken, <i>Gallus</i>	1-2-1-0-0	2-3-4-5-0
Dog, <i>Canis familiaris</i>	2-3-3-3-3	1-3-3-3-3
Pig, <i>Sus scrofa</i>	0-3-3-3-3	0-3-3-3-3
Cow, <i>Bos</i>	0-0-3-3-0	0-0-3-3-0
Horse, <i>Caballus</i>	0-0-3-0-0	0-0-3-0-0
Man, <i>Homo</i>	2-3-3-3-3	2-3-3-3-3

Amphibians

The posterior limb (Fig. 176) is usually of the typical tetrapod type with a single bone, the femur, in the first segment; two rather similar bones, the tibia and fibula, in the second segment; and the tarsals and foot bones in the third segment. The long bones of the first and second segments do not show much specialization, as in the higher vertebrates. In Anura, the tibia and the fibula tend to fuse.

The tarsals in urodeles tend to remain in an unmodified condition. Those of *Necturus* are often not well ossified and may be difficult to determine. *Ambystoma* has a more complete set of tarsals composed

of the tibiale, intermedium, and fibulare in the first row; a centrale in the second row; and five tarsalia in the distal row followed by five metatarsals and five digits with two to three phalanges. *Necturus* and a few others have the fifth digit missing, but it is present in most amphibians.

Reptiles

In those reptiles (Figs. 172, 177, 178) that have not lost their limbs the limb bones are well developed. The femur is well developed in most reptiles and shows a pronounced head for articulation in the acetabulum. The tibia tends to become larger than the fibula. The tarsals tend to be reduced by fusion with each other. The turtle has the first row of the tarsals formed by a long bone containing fused tibiale, intermedium, fibulare, and several centralia. In some species the fibulare is separate. The distal now contains four tarsalia, the fourth bone consisting of the fused fourth and fifth tarsalia. Five metatarsals and five digits are present. The phalangeal formula is 2-3-3-3-3.

In lizards a similar arrangement is found. In the posterior limb of the lizard *Sceloporus* (Fig. 178) the first segment, formed by the femur, is rather long, an indication of well-developed locomotion. The femur has a rounded head

for articulation with the acetabulum and a single trochanter on the mesial side. The condyles at the distal end supply the articulation for the tibia and fibula. A small patella is present. The second segment, formed by the tibia and fibula, shows some progressive changes, since the tibia is enlarged and the fibula reduced in importance, although retaining a place in the articulation with the tarsal joint. The tarsus is somewhat simplified by a consoli-

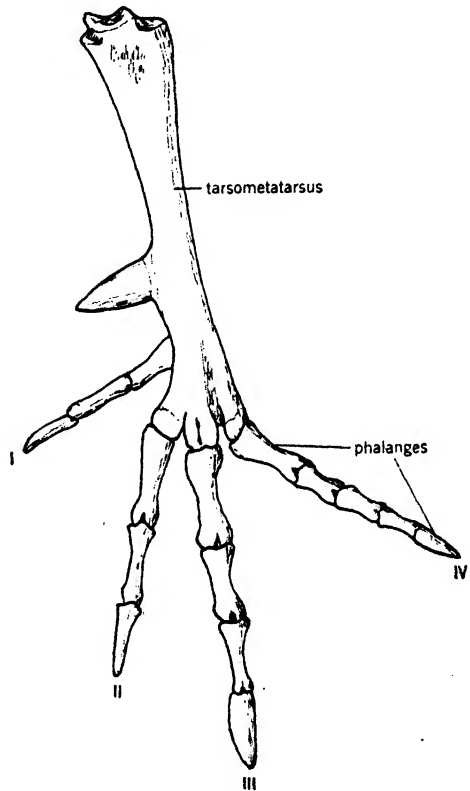


FIG. 186. The foot of chicken.

dation of bones. The proximal row consists of a single element formed by the tibiale, intermedium, and centrale, with a small separate fibulare. A small element on the mesial side of the tibiale probably represents a centrale. The distal series consists of but two elements, the first being tarsalia 2 and 3 and the second being tarsalia 4 and 5. Typical of the lacertilians, the fifth metatarsal is a peculiar hook-shaped bone. The phalangeal formula is 2-3-4-5-4.

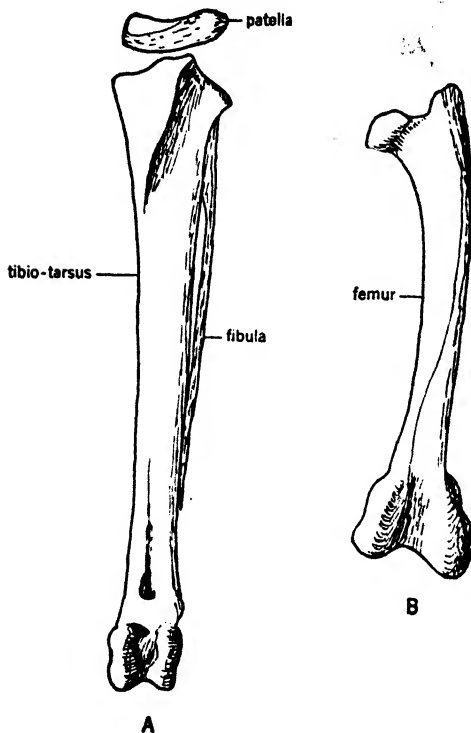


FIG. 187. A, tibiotarsus; B, femur of chicken.

Birds

The posterior limb (Figs. 186, 187) is marked by a fusion of the tarsals with the tibia and metatarsals. The femur, with a prominent articular head, is bird-like but not strikingly modified. A patella is present. The fibula is vestigial and is represented by a splint on the side of the tibia. The tibia is heavy and has fused with the proximal row of tarsal bones, forming the tibiotarsus. The metatarsals have fused together and have incorporated three distal tarsal elements, forming a single bone, the tarsometatarsus.

The only trace of the union of the metatarsals is seen in

the separate articular heads for each of the digits. These elements are separate in the embryo. Birds never have more than four toes, and some have reduced their toes to three or even two.

There is some question as to which toe is lost, the fifth or the first. The phalangeal formula of the toe bones is usually 2-3-4-5. In some birds the posterior or second digit has a small, partially developed metatarsal, which is attached to the others by a tendon.

Mammals

The posterior limb consists of the same number of segments as the anterior. The first segment is formed by the femur (Fig. 183),

a large heavy bone with a mesially extended neck and head which fits into the acetabular cavity. There are several trochanters for muscle attachments: the greater trochanter on the proximal head, a lesser on the inner side, and sometimes a third on the outer side of the shaft. The distal end has two condyles which articulate with the tibia. Between these condyles is a smooth groove for the patella, which is a sesamoid bone developed in the tendons. Several small fabellae, also sesamoid, are found just posterior to the knee joint.

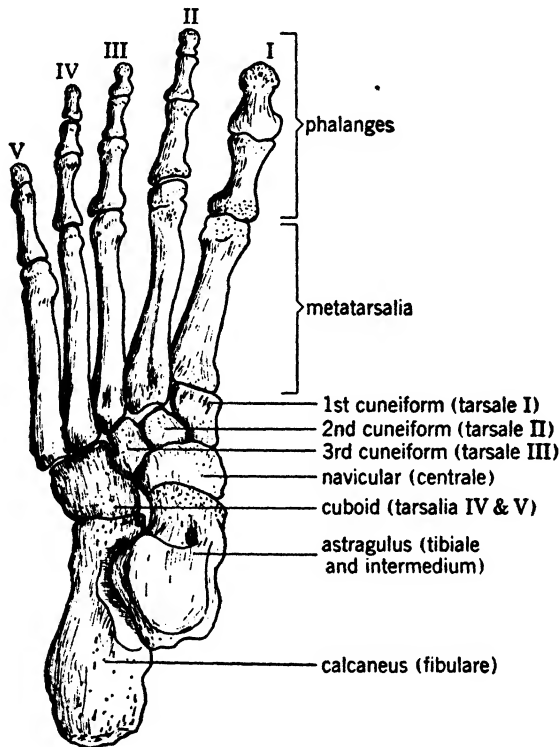


FIG. 188. Bones of human foot.

The second segment has two bones, the tibia and the fibula (Fig. 184). The main part of this segment is formed by the tibia. The fibula, usually more or less reduced, in the rat is ankylosed to the distal third of the shaft and is free only on the upper two-thirds. In ungulates, it becomes a vestigial splint. The tibia is large and has a sharp anterior edge, the cnemial crest. The proximal end articulates with the femur, and the distal end with the astragalus (talus). The small free end of the fibula may have a slight articulation with the astragalus.

There is a decided shift of position in the proximal row of tarsal bones, so that, instead of being side by side, the talus (astragalus) is anterior to the calcaneus (fibulare), which is on the sole of the foot. The astragalus is interpreted in several ways as a combination of the tibiale and centrale, or of the intermedium and centrale. The astragalus which is flat in the monotremes and marsupials, becomes keeled on

the surface that articulates with the tibia; this construction prevents slipping in this important joint (Figs. 180, 188).

The arrangement of the tarsals varies somewhat in different species of mammals. The human tarsals (Fig. 188) consist of the fibulare (calcaneus) or the large heel bone; the fused tibiale and intermedium forming the astragalus for articulation with the tibia. Anterior to the astragalus is a large centrale (navicular). The distal row contains four bones arranged as follows: the first tarsale (first cuneiform), the second tarsale (second cuneiform), the third tarsale (third cuneiform), and the fused fourth and fifth tarsalia (cuboid). Five metatarsals are present forming the foot and each supporting a digit with a phalangeal formula 2-3-3-3-3. The same arrangement occurs in the rat. The cat has the same arrangement of tarsals, but the first metatarsal is vestigial and

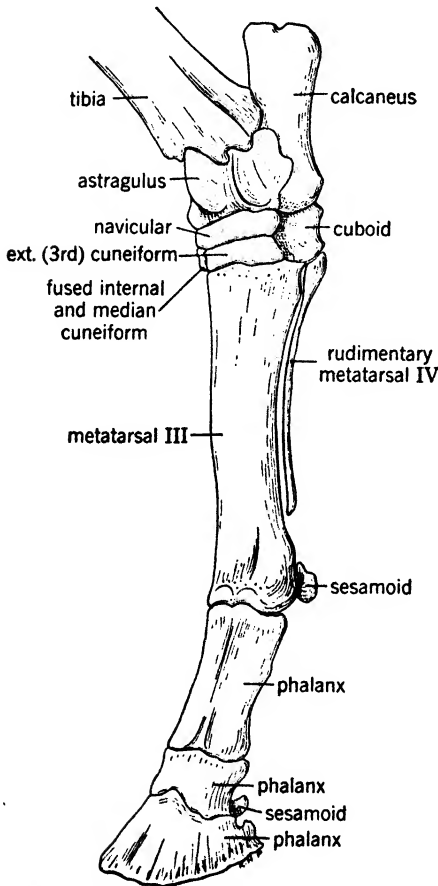


FIG. 189. Left hind foot of the horse.

the first digit is absent. The rabbit lacks the first metatarsal and has the first cuneiform fused to the proximal end of the second metatarsal.

Mammals that walk on their toes tend to have the calcaneus elongated. Ungulates have greatly modified their hind feet. The horse (Fig. 189) has a well-developed calcaneus and astragalus. A flat navicular lies just distal to the astragalus. A cuboid, a large flat third

cuneiform, and a small bone representing the fused first and second cuneiforms form the distal row and articulate with the third metatarsal, which bears one digit with three phalanges. Two vestigial metatarsalia are present as splints. Several tiny sesamoid bones are present on the posterior base of the digit. In the ruminants, two functional but fused metatarsalia are present and support two complete digits of three phalanges each. Two other digits are represented by vestigial metatarsalia and phalanges.

The Cetacea and the Sirenia have lost all their hind limbs and retain only a vestige of their pelvic girdles.

Articulations or Joints

Bones that articulate to any great extent are bound together by ligaments. Ligaments are related to tendons but are elastic and are not concerned with muscle attachments. Several types of ligaments occur in the vertebrate body, the most important is the type connecting skeletal parts. In many joints these ligaments enclose a joint capsule composed of a ligamentous sheath, lined with a synovial membrane and containing a lubricant, synovia.

The vertebrate skeleton is composed of numerous bony or cartilaginous elements, some of which are securely fused or ankylosed together; others have a slight movement or just enough to give resiliency, whereas those with free movement are supplied with ligaments and synovial membranes, with joint capsules and bursae filled with fluid to enable them to work smoothly. Two skeletal structures joined end-to-end must have some devices to give strength if the joint bears much stress. Muscles, tendons, and ligaments aid in making these joints strong and stable, but greater strength is achieved where joints have specialized surfaces to prevent side-play and slipping.

There has been a gradual increase in the perfection of the joints throughout the vertebrate groups until the most complex and efficient joints are developed in the birds and mammals. Three major types of joints are found in the vertebrates: the freely movable or diarthroidal joints; the slightly movable or amphiarthroidal joints; and the immovable or synarthroidal joints.

Diarthrosis

The diarthroidal joints are of many types, but all have articular surfaces covered by synovial membranes and are bound together by ligaments. The simplest, as well as the weakest, are those joints in which two flat surfaces slide over each other as in the ankles and wrists of man. In these joints the strength depends entirely on the pattern of the ligaments, which alone hold the bones in place. Many

joints are modified so as to form stronger articulations by means of locked surfaces. In such joints the surfaces are modified so that one may be slightly convex, the other slightly concave, and a medial ridge, and an opposing groove also may occur. This type appears in the knee joint of man and in that between the phalanges of the artiodactyls.

A more complicated type of locked joint occurs between the ulna and humerus of higher tetrapods, where the humerus articulates in a deep notch of the ulna, allowing movement in one plane only. A ball-and-socket joint allowing pivoting movement in all planes occurs between the humerus and the scapula and between the femur and the pelvis. A twisting movement, pronation and supination, is accomplished by the radius of man through a rather loose joint against the humerus and in a special groove on the ulna, allowing a possible twist of 180 degrees.

Amphiarthrosis

Amphiarthroidal joints allow slight but not free movement, are bound together by ligaments, but have no special synovial surfaces. In fishes, many bones of the skull and of the girdles are bound together and have no free movement, but their joints are somewhat pliable under stress. In many tetrapods such joints occur between the ischium and the pubis, between the sacrum and the ilium, and between some vertebrae. In higher tetrapods a peculiar joint of this type occurs between the ribs and the sternum. In mammals there are considerable movements in this joint through the cartilaginous connections, but there are no articular surfaces.

Synarthrosis

Synarthroidal joints are those between bones that have no synovial surfaces, and where no normal movement occurs. If such bones are joined by ligaments, it is only weakly. In old age such joints tend to fuse or ankylose, a process that removes them from the class of joints. The bones of the mammalian skull show many such joints usually called sutures.

Peculiar Bones

Sesamoid bones are ossified parts of tendons associated with joints in limbs, though not a part of the skeletal system. They form smooth bearings for muscle action over joints. In man the knee cap is a sesamoid, as also is the pisiform element of the proximal row of carpal bones, which articulates with the ulnare by a definite facet. Small sesamoids called fabellae are on the posterior side of the knee joint. A variable number of sesamoids are found on the flexor sides of some

joints in the hands and feet. Sesamoid bones are frequently formed in the tendons of the legs of gallinaceous birds, such as pheasants and turkeys.

A few other bones in the body are not connected with the skeletal system. The os cordis, or heart bone (Fig. 190 *B*), developed in the heart of some ungulates (*Bos*), may be of some size but is irregular and

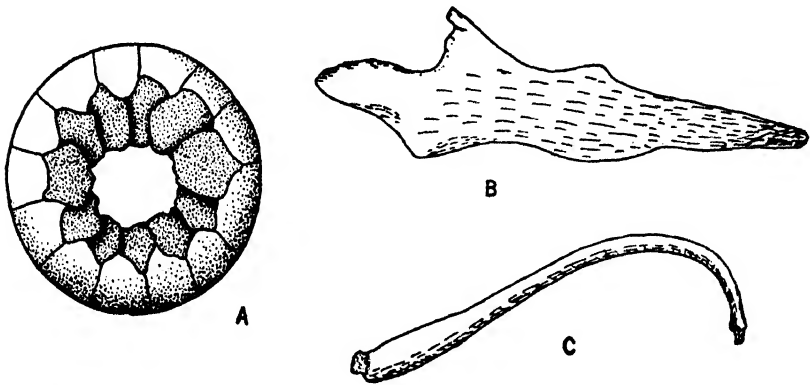


FIG. 190. Peculiar skeletal elements. *A*, sclerotic bones of lizard; *B*, heart bone (os cordis) of cow; *C*, penis bone (os priapi) of raccoon.

not of a fixed shape. In all classes except the mammals true osseous plates are formed in the sclerotic coat of the eye (Fig. 190 *A*), forming a ring or even a cup. The os priapi, or penis bone (Fig. 190 *C*), is found in the following orders of the mammals: Carnivora, Chiroptera, Pinipedia, Rodentia, Cetacea, Marsupialia, and lower primates.

Miscellaneous dermal bones in the form of skin plates are common among fishes and many fossil reptiles and amphibians. Dermal bones appear in a few mammals such as the armadillo and chevrotain.

CHAPTER TEN

Muscular System

The muscular and skeletal systems are closely associated and should be considered together because of their intimate relations. Most of the body muscles are attached to the skeleton; relatively few are fastened to other structures. Bones to which muscles are attached show clearly, in the development of processes, ridges, trochanters, and spines, the results of the strain imposed upon them by muscle pull. Limbs in which the muscles have atrophied, whether as a result of disease or accident, show not only a reduction in size but also differences in development associated with muscle attachment.

Types of Muscles

Vertebrates have three types of muscles which are developed from the embryonic mesoderm: (1) smooth, non-striated muscles, which are found in the walls of the digestive tract, and blood vessels, and in other organs of the body and are innervated by the autonomic nervous system; (2) voluntary or striated muscles, which make up the general musculature of the body and are under conscious control; (3) cardiac or striated muscles of the heart, which are not under conscious control and are peculiar in that they are able to function when all nerve connections have been severed. The smooth, non-striated type of muscles are phylogenetically the older. Both the involuntary smooth muscles and the cardiac muscles form parts of organs and are not treated as separate units anatomically. Only the voluntary striated muscles form individual masses that can be treated as separate organs. In comparative anatomy the term muscles usually refers to voluntary striated muscles.

Structure of a Muscle

The voluntary muscles are the "flesh" of a vertebrate. Muscle is built up by a multiplication of cells that have developed to a high degree the ability to contract under nervous stimulus. Each cell is a complicated unit made up of many nuclei and numerous branching striated fibrils, surrounded by a wall, the sarcolemma, and filled

with a fluid, the sarcoplasm. These units are in turn bound into bundles, and these bundles are bound to form individual muscles, which, by their connections to the skeletal structures and other parts, make movement possible. Each unit is supplied with its own set of blood vessels and nerves. It is possible for a muscle to contract to approximately one-half the length of its fibers.

Muscles are covered and bound together by a thin connective tissue known as fascia. At its ends, the muscle is attached to the skeleton or to some other structure by tendons, which are continuous with the fascia. Connective tissue that forms a thin sheet instead of a tendon is termed an aponeurosis. An aponeurosis forms the attachment of muscles in the mid-ventral line of the human abdominal wall (Fig. 196). The diaphragm of mammals originates from the thoracic walls and ends in a central aponeurosis.

A muscle has three parts: the belly or body, which is the central part of the muscle, and the two ends, one of which forms the origin and the other the insertion.

The origin of a muscle is generally its attachment to a fixed part; its insertion is on a structure to be moved. These criteria usually make it easy to determine the origin and insertion, but in some cases both the origin and insertion are on movable parts, as in a number of the head muscles in snakes, and here it is necessary to make comparisons with forms in which specialization is not carried to an extreme. Both origins and insertions may be complicated by splitting, so that they are multiple, as in biceps, triceps, quadriceps, etc. Multiple origins are called heads, and multiple insertions if in segmental sequence are known as slips.

In judging the homology of muscles in different classes of vertebrates a number of criteria are used, but no one is certain. The origins and insertions may change, muscles may drop out altogether, and subdivisions or splittings may occur. Generally the innervation can be trusted, although its interpretation is often difficult and sometimes doubtful.

General Arrangement of Muscles

Muscles are generally arranged in opposing sets—a necessary arrangement because their only action is contraction. A few muscles are sufficient for a simple movement, but a much greater number is required for a wide range of movements. The application of power falls into the three classes of leverage: the first is illustrated by the skull on the neck vertebrae, the second by the pull of Achilles' tendon on the heel, and the third by the pull of the biceps on the forearm (Fig. 191).

Muscles are extremely variable, assuming many forms, often shifting their original position and migrating to new ones. The stapedius muscle of the ear seems to be a slip of the levator hyoidei that has split off and followed the stapes into the ear. There has been much splitting of muscle masses. For example, the levator muscle of the fish becomes the levator mandibularae, moving the mandible, which in turn splits into the masseter and temporal, each of which may split again. The internal and external pterygoids appear to have split from this adductor mass. The digastric (p. 248) is a muscle of two origins, as shown by the double innervation, the anterior belly innervated by a branch of the trigeminus and the posterior belly by the facialis. Combinations of muscles generally show a tendinous area, the *inscriptio tendinea*, where the joining has taken place. The rectus abdominis shows these inscriptions very clearly.

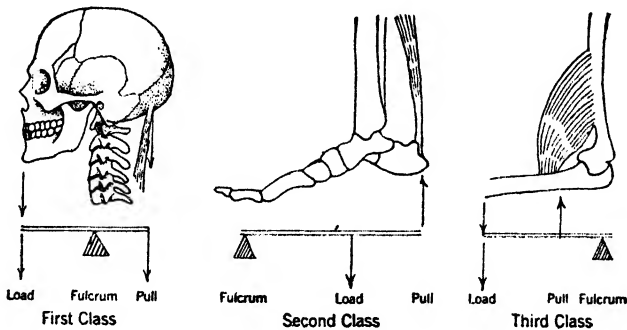


FIG. 191. Diagram of levers and their relation to muscle pull. From Morris after Testut.

One of the striking modifications of muscle tissue is its development into an electrical organ in some of the fishes, such as the electric rays, eels, catfishes, and some other teleosts. The electrical areas of these fishes are made up of modified muscle cells, supplied with a heavy innervation, from the spinal or cranial nerves. Some fishes are able to give an electric shock capable of stunning medium-sized animals.

Muscles function not only in movement but also in support of the skeleton, and in this they are very important. A difference in muscular tonus reacts quickly on the animal, and it is easy to note the difference in the carriage and attitude of an animal in perfect condition and one weakened by disease. The shoulder and pelvic joints, while bound by ligaments, are also well secured by the muscular attachments. In describing the action of a muscle, it is sometimes necessary to take into consideration the different positions of the structures concerned, for the action may vary with the position of the part. The contraction of a

muscle may have a single definite effect when acting alone, but quite different effects when acting in combination with others. Most movements are the effects of several muscles acting in combination.

Classification of Muscles

Muscles can be divided as to origin into the branchiomic, which is the visceral or gill musculature (Fig. 192) derived from the pharyngeal wall and is innervated by cranial nerves; and the myomeric or myotomic musculature, derived from the myotomes of the somites. The branchiomic muscles are derived from the hypomere and are primi-

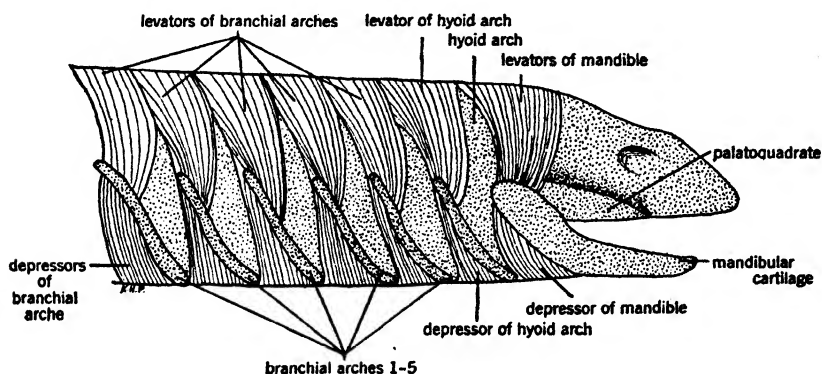


FIG. 192. Hypothetical diagram of primitive branchiomic musculature.
Redrawn from Wilder.

tively associated with the gills. The myomeric muscles and their derivatives are derived from the epimere and give rise to most of the trunk muscles. In the primitive vertebrates the myomeric muscles were more or less confined to the somites which range the entire length of the body as in *Amphioxus*. Fishes retain much of this primitive musculature. In the higher vertebrates these myomeric muscles have given rise, by various means, to some of the head muscles including those of the eye, the appendicular muscles of the girdles and limbs (at least in fishes and probably in tetrapods), the diaphragm muscles of mammals, and the integumental or dermal muscles of reptiles, birds, and mammals.

Embryology of Muscles

The myomeric or myotomic muscles are derived, embryologically, from mesoderm of the epimere and are basically metameric even in birds and mammals, where the primitive segmental arrangement is retained by only a few muscles, such as the intercostals between the

ribs. The branchiomic musculature, which originated in connection with the primitive gill arches, differs from the myomeric musculature not only in nerve supply, but also in the fact that it develops from the hypomere rather than from the epimere. Anteriorly the hypomere extends into the gill region, where any coelom formed tends to be obliterated, and the splanchnic wall, which posteriorly gives rise to smooth muscle of the gut, gives rise to striated muscle surrounding the pharynx. In fishes these muscles are associated with the gills and jaws, but in land vertebrates they are confined to certain muscles mostly concerned with the mandible and other derivatives of the gill arches.

Myotomes or Myomeres

Although myomeric segmentation in the region of the head is obscure among living vertebrates, the myomeres and myosepta of the somatic or trunk musculature are conspicuous in the bodies of fishes and some amphibians. The myotomes or muscular segments are separated by the chevron-shaped myosepta or myocommata, between which the muscle fibers run longitudinally and to which the fibers attach. The myotomes and myosepta are divided longitudinally in the fishes in the region of the lateral line by a septum which extends from the axial skeleton to the integument, dividing each myomere into a dorsal epaxial and a ventral hypaxial region. In primitive vertebrates the apex of the angle of the chevrons falls on this dividing septum. In more advanced forms, the myotomes and separating myocommata become more complex, and each arm of the chevron tends to assume a zigzag arrangement. The epaxial muscles or dorsal parts of the myotomes give rise to the back muscles of the tetrapods, and the hypaxial muscles or ventral part of the myotomes gives rise to the abdominal wall (Fig. 193) and other ventral muscles of the tetrapods.

Head Muscles

The head myotomes show a prootic series of three somites and a postotic series of a variable number. The dorsal parts of these myotomes disappear; skull development apparently suppresses their formation. Even the original segmental arrangement of the nerves serving the head segments is obscured by the combination of several nerves into a single element, such as the vagus, which represents a number of segmental nerves joined together. The first three prootic myotomes supply the eye musculature (Fig. 194): the first myotome splits to form the superior, inferior, and internal recti, and the inferior oblique, all of which are innervated by the oculomotor nerve (III); the second

myotome forms the superior oblique innervated by the trochlear nerve (IV) and part of the external rectus (Fig. 194); the third myotome forms the rest of the external rectus which is innervated by the abducens nerve (VI). This nerve (VI) has shifted its position to a myo-

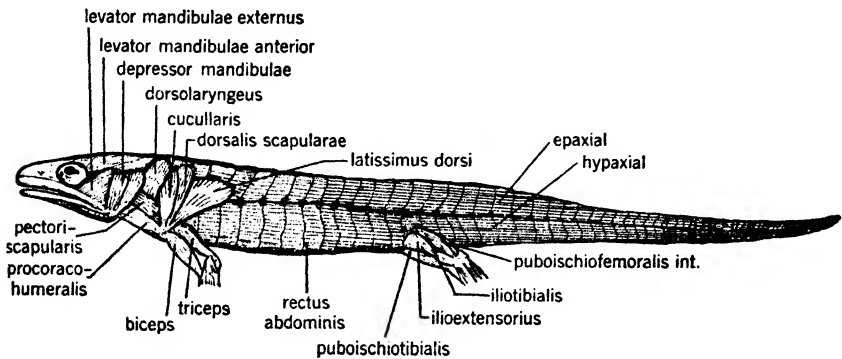


FIG. 193. Lateral musculature of *Ambystoma*.

tome anterior to its original embryological position—an interesting development, for shifts in the innervation of a muscle are rare.

In cyclostomes the fourth myotome gives rise to the first permanent trunk myotomes. In elasmobranchs, the myotomes of the fourth,

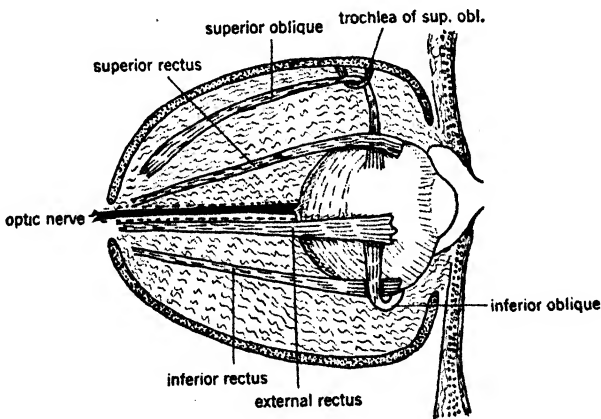


FIG. 194. Mammalian eye muscles, showing pulley arrangement of superior oblique. After Plate.

fifth, and sixth somites form connective tissue. The seventh myotome gives rise in the sharks to the first permanent trunk myotome. The postbranchial myotomes are related to the hypobranchial musculature. Buds from the ventral ends of the postmandibular myotomes migrate forward to form the hypobranchial muscles, which become associated

with the gills in fishes and form certain throat, neck, and tongue muscles of higher vertebrates.

Branchiomic Meric Muscles

The branchiomic muscles, arising from the hypomere in the region of the pharynx, served originally with the hypobranchial muscles to move the gill arches (Fig. 192). The gill arches are moved by a series of depressors and levators, some of which have been derived from the branchiomic muscles, others from the hypobranchial muscles. The innervation of these branchiomic muscles is through the cranial nerves, the first or mandibular segment by the trigeminal, those of the second or hyoid by the facial, those of the third by the glossopharyngeal, and those of the remaining arches by the vagus.

In fishes these muscles are highly developed. With the shift of the first arch to form the upper and lower jaws, its branchiomic muscles became jaw muscles. The gills of the shark are supplied with a musculature that gives considerable movement to the individual gill arches. The dorsal and ventral constrictors raise and lower the gills; within the individual gill arch, a series of small muscles—the interarcuales, the adductor arcuus branchiales, and the interbranchiales—give further action. The ventral region of the gill arches has a number of long muscles connecting it with the mandibles and the coracoid cartilage. Both the coraco-mandibularis and the coraco-hyoideus muscles assist in movement of this basal region by tensing or relaxing the ventral wall.

The highly specialized musculature required for movements of gills is much simplified or lost in the land tetrapods. The branchiomic muscles of the first visceral arch, which became the simple levator of the fish jaw, divides, forming the masseter and the temporal muscles as levators of the tetrapod jaw (Figs. 195, 199, 200). The mammalian digastric, which is a depressor of the jaw (Figs. 199, 200), is derived partly from the branchiomic muscles of the first arch and partly from those of the second or hyoid arch. Lateral and posterior movements of the jaw are made possible by different combinations of these muscles assisted by two small muscles, the internal and external pterygoids, which are also derived from the branchiomic muscles of the first arch. Some of the small muscles associated with the incus and the malleus, derivatives of the quadrate and articular, are also derived from the branchiomic muscles of this same arch. A broad sheet of branchiomic muscle, the mylohyoid (Fig. 199), extends between the mandibles, acting as a constrictor for the throat by raising the floor of the mouth.

The branchiomic muscles (Fig. 192) of the other gill arches are

partly lost in the tetrapods with the loss of the gills, but many muscles are retained and serve the derivatives of those arches, such as the hyoids and the laryngeal cartilages. The posterior part of the mammalian digastric is a vestige of a branchiomic muscle, interhyoideus, once connected with the hyoid arch. The stapedius was a levator of the second arch and has followed the hyomandibular into the middle ear, occurring in mammals as a tiny muscle associated with the stapes. The constrictor coli of lower tetrapods gives rise to part of the platysma of mammals (Fig. 204). Branchiomic muscles of other arches have divided to form some of the neck muscles of higher tetrapods, such as

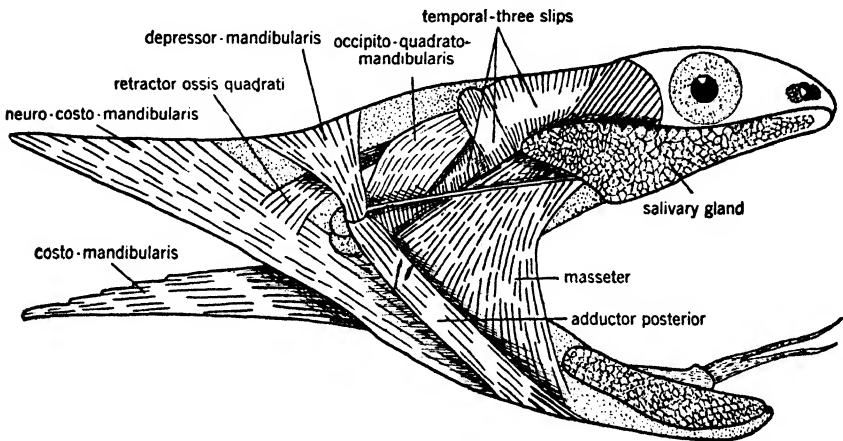


FIG. 195. Musculature of snake head (*Natrix*).

the trapezius, various modifications of the sternocleidomastoid, and the branchiohyoid muscles of mammals. The musculature of the tongue becomes highly specialized by the additional development of an intrinsic set of hypobranchial muscles.

Myomeric Muscles

The most primitive condition of the myomeric muscles can be seen in *Amphioxus*, where they constitute an unbroken series of myotomes from head to tail. In the cyclostomes, they still retain much of their original segmental arrangement. The hypobranchial muscles of the gill arches appear from buds from postbranchial myotomes, which migrate forward to the gills. In higher vertebrates, these muscles give rise to some of the tongue and throat muscles. In the elasmobranchs, the myotomes become divided transversely into an upper epaxial and a lower hypaxial set of muscles. The musculature of the fishes is strictly segmental except in the regions of the head and in the pectoral

and pelvic fins. In general the musculature is rather simple but shows some of the specializations that are to occur in the tetrapods. The head myotomes have already become very highly specialized. The trunk and tail myotomes are retained very distinctly, except where they are distorted to permit the muscles of the fins to reach the inner parts of the pectoral and pelvic girdles. The appendicular muscles

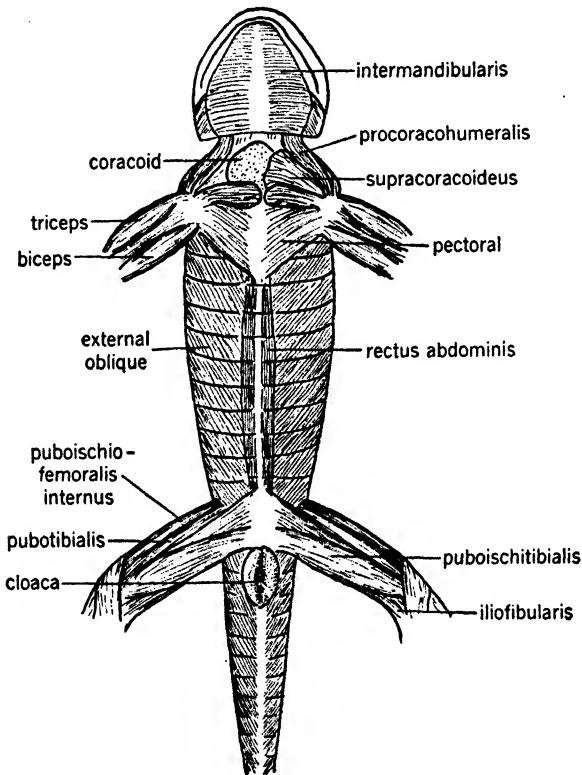


FIG. 196. Ventral musculature of *Ambystoma*.

have become differentiated and are beginning to encircle the body both dorsally and ventrally, thus partially covering the original myotomic system.

The epaxial and hypaxial divisions of the myotomes (Figs. 193, 196) can be traced into the urodeles but are lost as the myotomes are obliterated in the reptiles, birds, and mammals, although muscles derived from these divisions can be traced. The muscles of the higher vertebrates tend to become specialized, and, with the great development of the appendicular muscles, the original myotomic arrangement is lost, except in a few cases, such as the *serratus magnus* and the

rectus abdominis. Their original relations may be traced through their innervation, although migrations and splittings have often completely changed their original position.

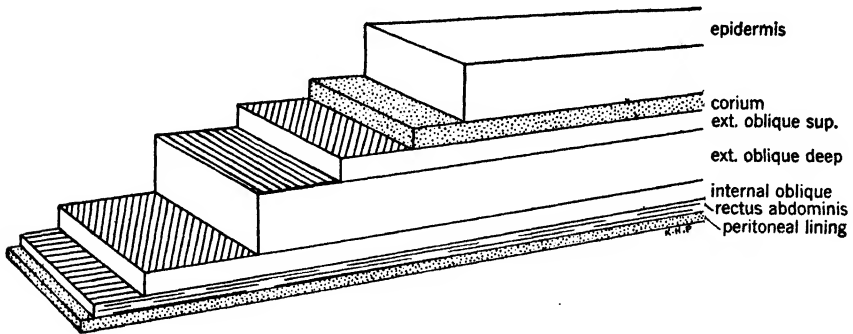


FIG. 197. Diagram of the layers of the body wall in *Ambystoma*.

The epaxial divisions of the myotomes have given rise to the back muscles of the tetrapods, such as the multifidus and the longissimus dorsi series. The hypaxial portion of the myotomes has given rise to the ventral abdominal wall muscles, which consist of the external

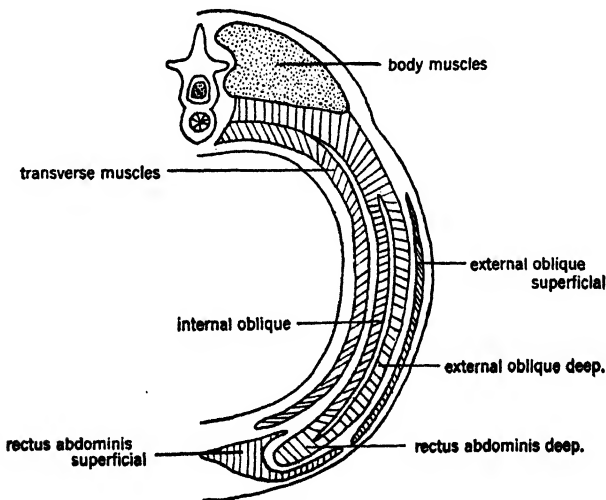


FIG. 198. Cross-section of body wall to show musculature. After Büchli.

oblique, the internal oblique, the rectus abdominis, and the transverse abdominis. The muscular sheets of the body wall (Fig. 198) are so arranged that their fibers extend in different directions, thus giving added strength and great powers of compression. From the myotomes, the appendicular muscles of fishes and the integumental

muscles of tetrapods have developed and in the higher vertebrates form a conspicuous part of the musculature.

The skull is attached to the cervical vertebrae by ligaments and also by a series of muscles, some short and some long, that assist in

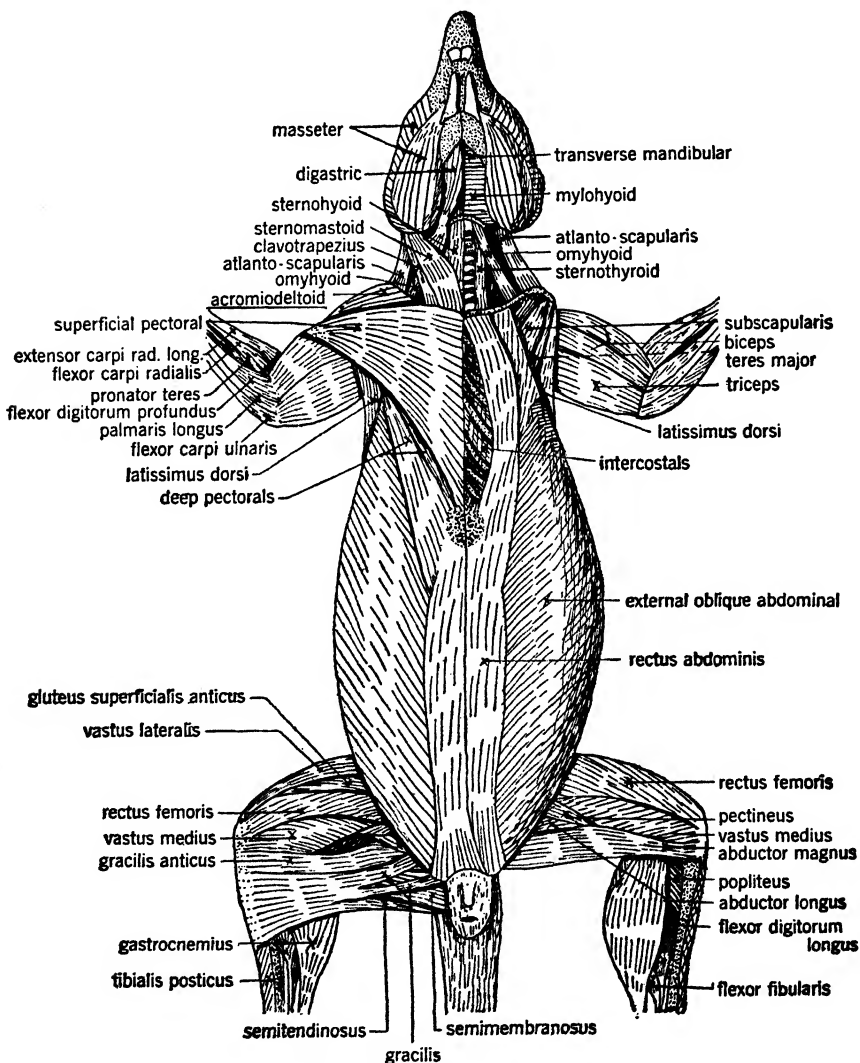


FIG. 199. Ventral musculature of a wood rat. Redrawn from Howell.

holding the head in position and in giving it freedom of movement. These short muscles are the rectus capitis and the oblique capitis, which originate on the atlas and axis. The longer muscles are the longissimus capitis, semispinalis capitis, and the splenius capitis, which originate

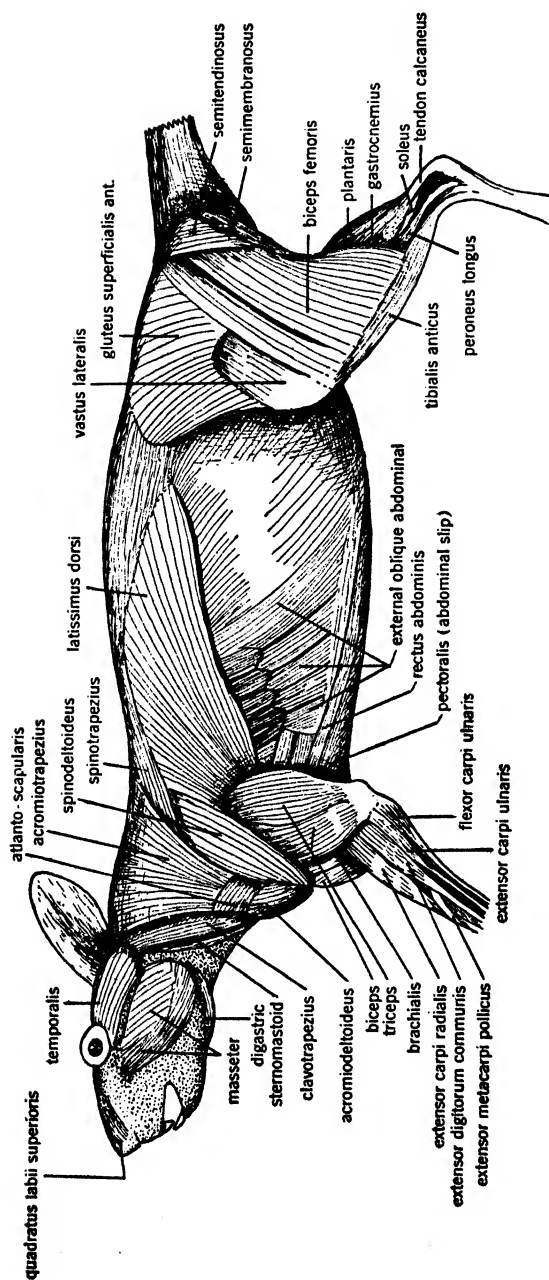


Fig. 200. Lateral muscles of wood rat. Redrawn from Howell.

on the cervical vertebrae and are inserted on the occipital region of the head. The large posterior trapezius connects the skull with the clavicle and scapula (in man), and more anteriorly the sternomastoid and cleidomastoid connect the sternum and clavicle with the skull (Figs. 199, 200).

In the tetrapods, many hypobranchial muscles, once associated with the branchiomic muscles in moving the gills of fishes, form important neck, throat, and tongue muscles (Fig. 195). These hypobranchial muscles have originated from buds of the postbranchial muscles that have migrated forward. The sternohyoid, omohyoid, and the thyrohyoid (Fig. 204) are derived from the rectus cervicis, a con-

tinuation of the rectus abdominis. The geniohyoids, hyoglossus, genioglossus, and styloglossus, muscles of the hyoids and tongue, are derived from these postbranchial buds.

The spinal column is supplied with a series of short muscles between individual vertebrae and with a series of longer muscles between the regions of the column. Besides the vertebral system proper, there are series of muscles connecting it with other movable parts, such as the girdles and limbs, and series of intercostal muscles between the ribs to assist in breathing.

Appendicular Muscles

The appendicular muscles are the muscles of the girdles and the fins or limbs. These first appear in fishes; they arise in some fishes from myomeric buds which move to the girdles and out into the fins (Fig. 201). In the tetrapods the muscles of the limbs do not arise in the embryo from buds off of the myotomes but develop from migrating cells. However, their similarity in innervation indicates that they are homologous to those of fishes and must have

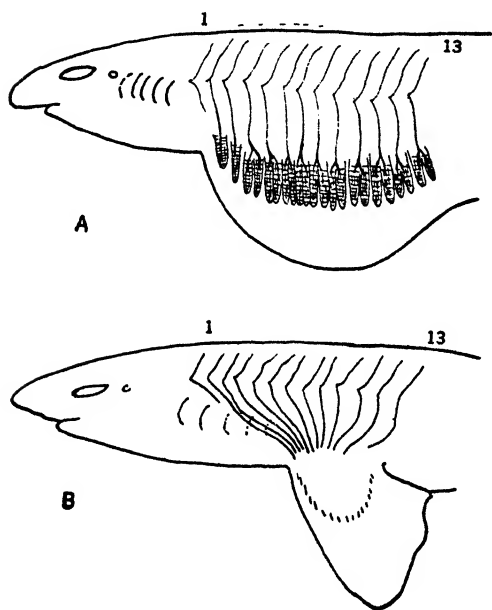


FIG. 201. Diagram showing the formation of limb buds in development of shark. A, adult condition, with muscles and nerves artificially spaced to show relations. B, adult condition with muscles and nerves naturally grouped. After Goodrich.

had a similar phylogenetic origin. These muscles, which are relatively few and small in the fishes, reach great size and very high development in the tetrapods. They can be divided in both fishes and in tetrapods into intrinsic and extrinsic muscles. Extrinsic muscles are those that have their origin within the trunk, although their insertion may be in the limb. They include the muscles of the girdles and the proximal segment of the limb. Intrinsic muscles are those that have both their origin and insertion entirely within the limb; they include the muscles of the distal segments.

The growth of the myotomes into the limb buds also shows a shifting of muscular material (Fig. 201). In the developing fins of sharks, a number of buds from the myotomes with their segmental nerves force their way into the developing limb, bifurcating to supply the mesial and lateral sides. There is a wide variation of the number of myotomic buds concerned in the building of the appendicular musculature, and this explains their peculiar innervation and nerve plexus.

In the lower tetrapods the pectoral girdle may be closely articulated with the sternum through the coracoids and clavicle, but in the mammals the connection of the girdle is entirely by ligament and muscle, except in those forms in which a clavicle is present. (In these mammals the clavicle connects the scapula and the sternum.) By means of the large superficial trapezius muscle, the scapula is attached strongly to the vertebral column and also to the skull. In addition the scapula is moved by a series of muscles that connect it with the body, such as the levator scapulae, serratus magnus, and the rhomboid series (Fig. 200). These working in combinations elevate, depress, adduct, and abduct the scapula, so that the musculature is admirably adapted to give a maximum of movement in the shoulder joint. Since both the purely scapular muscles, as well as the humeral muscles, are concerned in the movement of this part of the fore limb, the number of muscles in this region is large.

In the segments of the anterior limb, flexion, extension, adduction, abduction, circumduction, pronation, and supination are possible. The extension of the humerus is through the triceps on the posterior side of the arm, and flexion by the biceps, deltoid, and coraco-brachialis. Adduction, abduction, and medial and lateral rotation are made possible by the teres major and minor, subscapularis, latissimus dorsi, and pectoralis major, in different combinations (Figs. 199, 200). The pronator and supinator muscles act between the radius and the ulna.

In animals that make much use of their fore limbs, the forearm-carpus segment becomes highly specialized, with a wide differentiation of the musculature to the individual digits. Muscles extend to the carpus and also to the digits by means of tendons that reach to the

finger tips. Although the muscles have fleshy origins on the upper arm and forearm, only tendons are extended to the hand and fingers, thus keeping the wrist small and pliable. The extensor digitorum communis sends tendons to fingers 2, 3, 4, and 5, and additional extensors go to fingers 1, 2, and 5. The flexor digitorum sublimis is inserted on the proximal joints of the fingers; the flexor digitorum

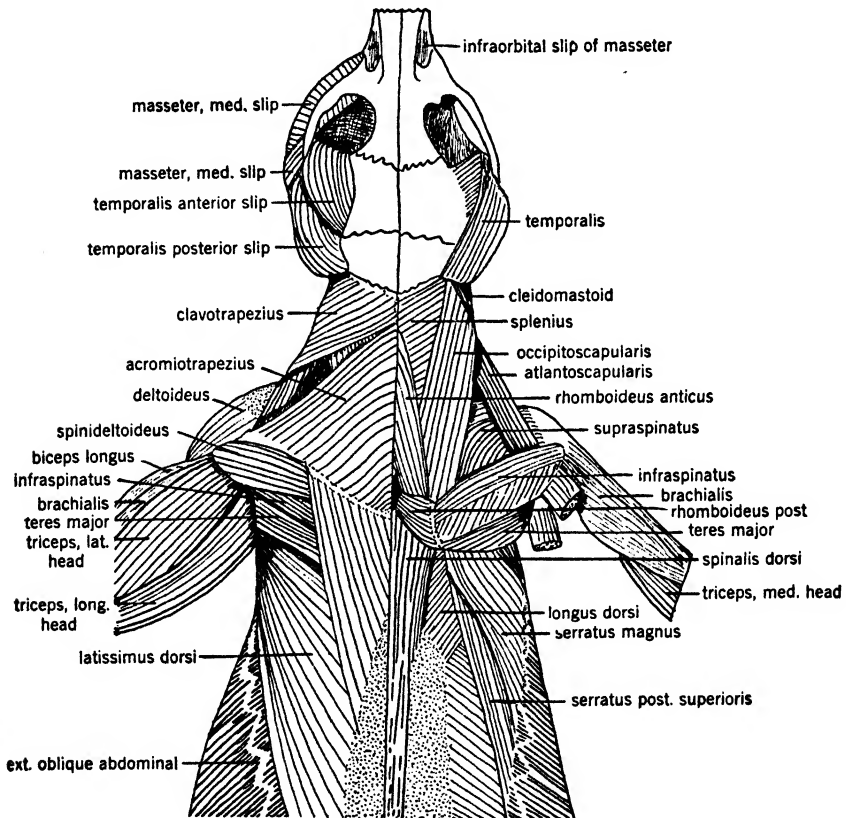


FIG. 202. Dorsal musculature of head and shoulders in wood rat.
After Howell.

profundus, a deeper muscle, is inserted on the proximal ends of the third row of phalangeal bones. Besides the large extensors and flexors, smaller muscles are supplied to the fingers, giving them strength and a greater variety of movement, as well as support, especially in the extended position.

The musculature of the posterior girdle consists first of muscles that are associated with the pelvis and the vertebral column, and secondly with the femur and other segments of the posterior limb. Both groups

are concerned in the flexion and extension of the pelvis. These movements are accomplished by working the muscles singly or in pairs. The principal muscles concerned in the flexion of the pelvis are the gluteals, hamstring muscles, and the abdominals. The extension group consists of the iliopsoas muscles, the adductors, quadriceps extensor, sartorius, and gracilis. Rotation is effected by different combinations of these muscles (Figs. 200, 203).

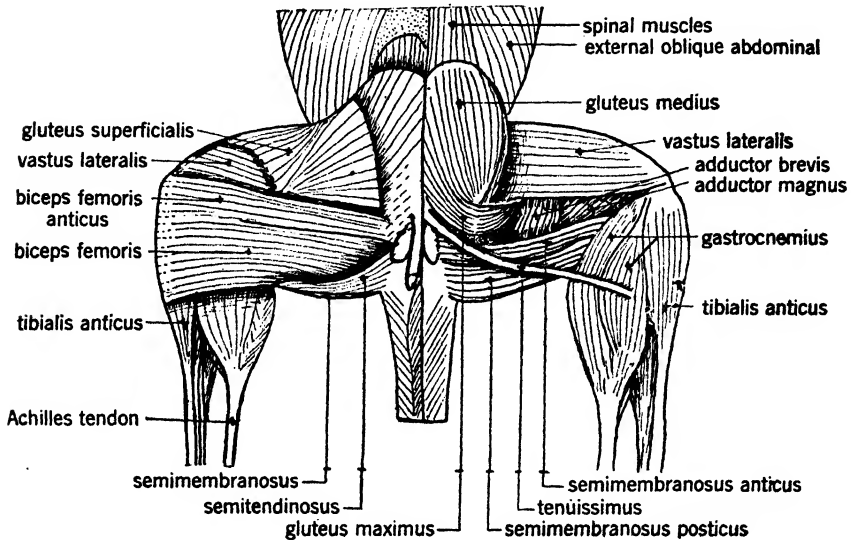


FIG. 203. Dorsal rump muscles of wood rat. After Howell.

The muscles of the femur, although not so great in number as those of the humerus, permit extension, flexion, adduction, abduction, rotation, and circumduction. The main muscle concerned in extension is the gluteus maximus, and in flexion the iliopsoas and pectineus. The abductors are gluteus maximus, gluteus medius, and gluteus minimus, piriformis, and tensor fascia; adduction is effected by the adductor longus, adductor brevis, and adductor magnus assisted by the pectineus and obturator externus (Fig. 203). Rotation of the femur is through combinations of these muscles, together with the action of the gemelli and quadratus femoris.

The action of the knee joint consists principally of flexion and extension, with but a limited amount of rotation. The extension is through the large quadriceps femoris, which consists of the rectus femoris and the three vasti muscles (Fig. 203). These end in a tendon which is attached to the proximal end of the tibia. Included in this tendon is the large sesamoid bone, the patella. The flexors of the leg

are numerous, consisting of the biceps, popliteus, sartorius, gracilis, semimembranosus, and semitendinosus (Figs. 199, 203). Amphibia and reptiles have possibilities of more rotation between the tibia and fibula than the higher animals, in which there is a tendency to ankylosis of the fibula with the tibia, with a reduction or almost complete loss of the fibula.

Because of the importance of the ankle joint, it is supplied with a very highly specialized musculature. Here the extensor muscles are the gastrocnemius, soleus, and plantaris, which unite to form the tendon of Achilles, and the tibialis posterior, peroneus longus, and peroneus brevis (Figs. 199, 203). Flexion, which is a weaker action, is through the peroneus tertius and tibialis anterior, and the extensors of the toes. The tibialis posterior and the three peroneus muscles are concerned in rotation, inversion and eversion of the foot.

There is a striking resemblance between the musculature of the foot and that of the hand. The foot is supplied with the usual possibilities of movement in animals in which there is no reduction of the digits, but in those with fewer toes there is a tendency to restrict the movements for mechanical reasons. Usually there is a possibility of rotation in the first and fifth toes when they are present. The extensor digitorum longus originates on the proximal end of the tibia, forming tendons at the ankle which supply all but the first toe, this being supplied by the extensor hallucis longus. A shorter muscle, the extensor digitorum brevis, originates on the calcaneus and acts as a short extensor. The toes are flexed chiefly by the flexor digitorum longus, which extends through four tendons to toes 2, 3, 4, 5. These same toes are also flexed by the flexor digitorum brevis. The first toe, or hallux, is flexed by flexor hallucis longus and brevis. The fifth toe has an additional muscle, the flexor digiti quinti brevis. Toes 1 and 5 have the greatest movement since they have some rotation. In apes there is considerable opposability of the hallux, but in man this character is reduced or lost.

The musculature of the feet varies greatly, because of the different ways in which they are used. In flat-footed plantigrade animals, which walk on the whole sole of the foot, there is great pliability in the individual parts, and often a tendency to form a bifurcate structure, in which two parts are opposed for grasping. Though plantigrade in structure, the foot of man is used to raise him on his toes in many activities. The digitigrade foot loses its independent action of the toes to some extent, and there is a corresponding simplification in the musculature. In the unguligrade foot, such as that of the horse and cow, the musculature is still more simplified and specialized, and the foot is greatly strengthened by reduction of lateral movement.

Integumental Muscles

Besides the musculature of the skeleton a system of superficial muscles is connected with the integument that moves the skin. These muscles are the integumental muscles which have originated by splitting off from the myomeric muscles, with the exception of some, such as the mammalian platysma, which have an origin from the branchiomeric muscles of the second visceral arch. Integumental muscles do

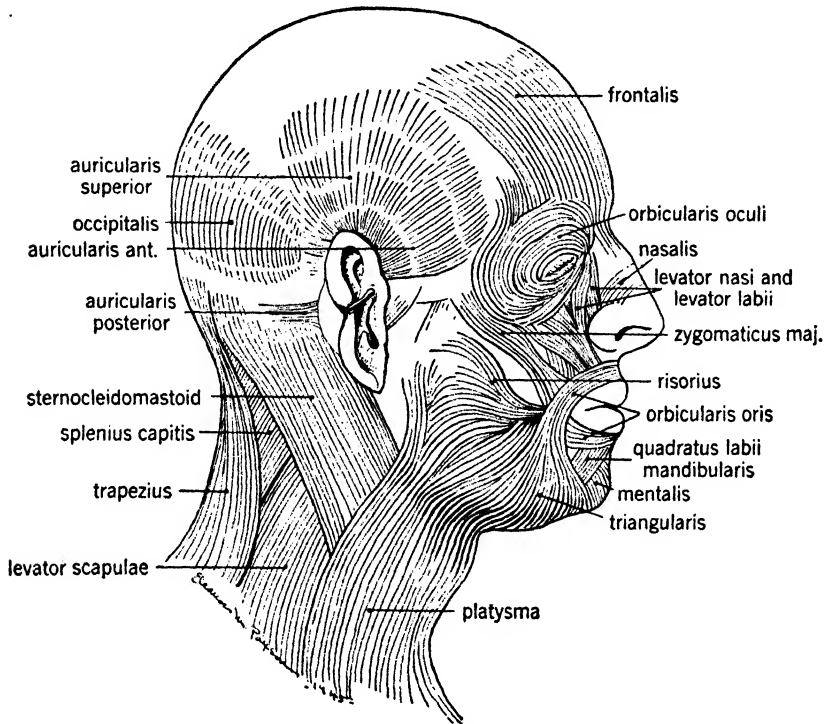


FIG. 204. Superficial muscles of the human head. Modified from Sobotta-McMurrich.

not appear in fishes and are poorly developed in amphibians. They are well developed in reptiles, birds, and mammals. Within the skin structure, small muscles in the corium move structures such as scales, feathers, and hairs. These are under the control of the autonomic system. In the region of the neck and face a superficial muscle layer, the sphincter colli of the reptiles and birds, acts to move the skin. In the higher animals it becomes much specialized and divided into a superficial platysma and a still deeper layer called the sphincter colli. From the outer sheet, the platysma, the facial musculature is developed, consisting of muscles that are concerned in the movement of the ears,

eyelids, nose, lips, and scalp. This facial system is highly specialized in mammals and extremely well developed in man and other primates. A second superficial system, known as the panniculus carnosus, is supposed to be a derivative of the latissimus and the pectoralis muscles. It may spread over the whole body or may be limited to the region of the axilla of the fore leg and the inguinal region of the hind leg. Its function is to enable the animal to shake the skin vigorously, to expel water, insects, or other foreign material from the skin and hair. The armadillo and manis make use of the sheet for rolling themselves into a ball.

CHAPTER ELEVEN

Digestive System

The digestive system consists of the alimentary tract and several associated organs. It is relatively uniform throughout the vertebrates, consisting of major regions or parts which are common to all. The major regions of the alimentary canal consist of the mouth, pharynx, esophagus, stomach, and intestine. Other organs associated with this system are the liver and the pancreas.

The digestive system is one of the earliest to develop. Early in the development of the embryo there is a differentiation of the ectoderm, or protective layer, and the endoderm, or digestive layer. Primarily, the digestive system consists of a simple tube, of which the ends, the mouth and rectum, are lined with ectodermal tissue and the rest with endodermal tissue. In the process of development, certain outpocketings occur which may be concerned in the digestive functions or may be associated with other activities of the body. The greatest problem of the system is to keep the absorptive area large enough to supply the bulk of the animal with sufficient food material, and for this reason the tube is never straight except in the simplest vertebrates.

Since the processes of digestion are very complex and since so many kinds of foods are used, there is much specialization of the parts to supply the area required for different activities. Even the simplest vertebrates have a mouth where the food is received, a stomach for the storage and action of the gastric juices, an intestine for further elaboration of the digestive processes and absorption into the venous system, and finally a posterior differentiation of the gut for the reduction of the waste by the removal of the excess water.

The processes of digestion consist for the most part of the simplification of the different complex foods utilized, since it is by this action that the materials are changed chemically so that they are simple enough to be absorbed by the cells of the body. Glands are located in most regions of the tube, the largest being the liver and the pancreas, which have so increased in size that they have withdrawn from the wall of the intestine and are now connected only by ducts. The general innervation is through the vagus nerve and the autonomic system.

The digestive activities may be considered under two main heads: (1) mechanical breaking up of food, and (2) chemical changes. Anatomical changes allow for each of these. The mechanical reduction of food is best accomplished in the mouth of animals that have teeth. If teeth are missing, as in birds and turtles, the food may be torn to pieces by jerking and tearing. In some turtles the esophagus is horny and thus assists in the reduction process, but by far the most effective arrangement in toothless animals is the division of the stomach into a glandular portion, or proventriculus, and a gizzard lined with a horny epithelium, which grinds the food to a pulp by means of stones or grit. Such gizzards are found in some reptiles and birds. By means of circular and longitudinal muscles in the walls of the stomach and intestine, peristaltic movements extend along the digestive tract, gently churning the food in the stomach and keeping it moving through the entire tube. Actually the teeth of many fishes, amphibians, reptiles, and mammals play a very small role in the reduction, regardless of their great importance in the grasping of food. Few mammals except herbivores chew their food beyond reducing it in size for swallowing.

The second stage, or digestion proper, consists of chemical processes by which foods with a complex structure are rendered simple. Special enzymes, such as invertase, ptyalin, lipase, amylase, and pepsin, act as catalyzers; that is, these enzymes take an active part in the transformation but are not used up in the ordinary sense and do not appear in the end products of digestion. The sources of digestive juices are the mouth, stomach, small intestine, liver, and pancreas, the last two contributing their products to the small intestine. The large intestine is generally not the seat of digestive action, although digestion of cellulose may take place there in animals eating food made up of this material. The reduction in this case is bacterial.

The main absorption of food takes place in the small intestine, although a slight amount may be taken from the walls of the stomach and also from the proximal end of the large intestine. The absorption into the blood is through the villi (Fig. 216) which line the walls of the small intestine, and from these the digested food is conducted through the veins of the mesenteries to the hepatic portal vein and the liver. As the blood passes through the capillaries of the liver, a part of its load of food is stored there, so that the general food content of the blood circulating over the body remains somewhat constant. Sugars thus extracted from the blood by the cells of the liver are stored as glycogen for future use. (The kidneys also serve to regulate the sugar content of the blood by taking out any large surplus.) The fats are taken from the small intestine into the lymphatic system through the villi and

are put into the venous blood stream through the thoracic ducts. (See the chapter on the circulatory system.)

The assimilation of food by the cells of the body is not possible until the blood is taken into capillaries where the plasma carrying the food can escape and come in direct contact with the cells themselves. From this plasma the individual cells are able to take up the material that they need and make it a part of themselves.

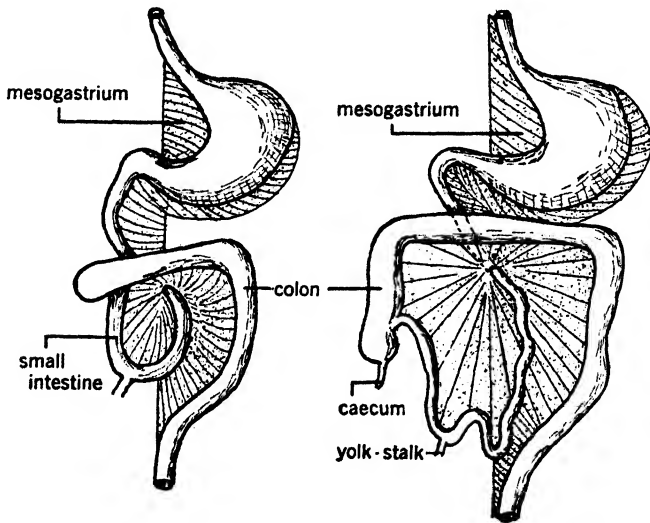


FIG. 205. Development of mesenteries in man. After Hertwig.

Coelom and Mesenteries

The digestive organs of the vertebrates lie mostly within the coelom or body cavity and are suspended by mesenteries. The coelom originates from the cavities of the paired coelomic pouches, cut off by the formation of the hypomere in the embryo. It is lined with a mesodermal epithelium known as the peritoneum. As these pouches arise on each side of the gut, the two inner walls come together, enclosing the digestive tract and other organs. The union of these median walls forms a double-layered membrane, the mesenteries. The mesentery is continuous with the peritoneum and forms the covering of all suspended organs, becoming the serosa or visceral peritoneum.

The main mesentery supports the digestive tract, by which it is divided into a dorsal and ventral part. Because of the horizontal position of the vertebrate body, the ventral mesentery has little function and tends to disappear, leaving the dorsal part as the chief supporting structure. In most vertebrates, the remnants of the ventral mesentery can be seen in the falciform ligament, extending from the

body wall to the liver, and in the mesentery extending from the liver to the stomach.

The dorsal mesentery is divided into several parts and, because of the coiling of the intestines, becomes so folded that it appears quite

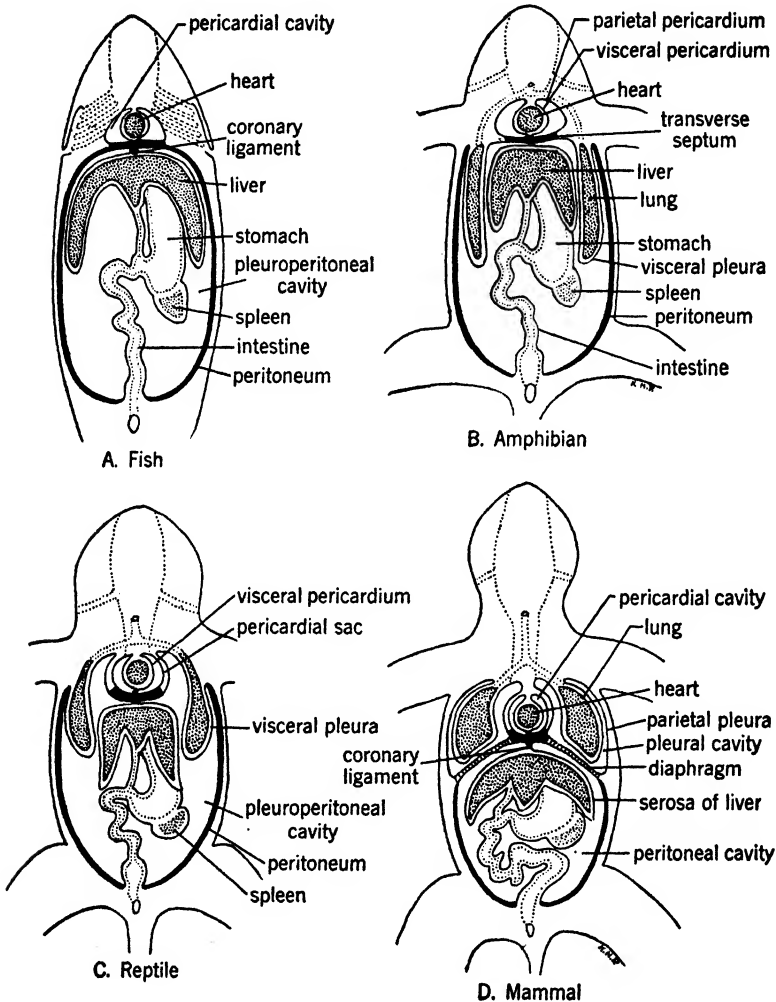


FIG. 206. Diagram showing the change of position of the organs as the heart and lungs push back, with the formation of a diaphragm.

complex (Fig. 205). The spleen is attached to the stomach by a fold of this mesentery. The gonads and their ducts are pushed out of the body wall in a peritoneal fold and thus become suspended in a series of mesenteries.

Coelom

The coelomic cavity extends only through the trunk region in adults, becoming divided early into a small anterior and a larger posterior region by a transverse wall. In sharks (Fig. 206), this wall is the transverse septum, which separates the heart from the rest of the viscera. The anterior part of the coelom becomes the pericardial cavity, and the larger posterior portion becomes the pleuroperitoneal cavity.

In Anura and most reptiles, the lungs lie within the pleuroperitoneal cavity and the pericardial cavity pushes posteriorly and lies between the lungs.

In crocodiles, birds, and mammals there is a further division of the pleuroperitoneal cavity. Folds push across to unite with the old transverse septum at the posterior end of the pericardial cavity, forming a pair of cavities containing the lungs. In birds this new septum is known as the oblique septum. In mammals, muscular elements move out into this new septum and form the diaphragm (Fig. 206), which thus has a central portion derived from the old transverse septum, and a peripheral portion formed of mesenteric and peritoneal folds, into which muscles have migrated.

In birds and mammals there are four divisions of the coelom: the pericardial cavity, right and left pleural cavities, and the peritoneal or abdominal cavity. Because of development of the lungs and the posterior shifting of the heart in the higher vertebrates, the stomach, liver, spleen, and other visceral organs have been pushed farther back so that, in mammals, they are about in the middle of the trunk. In fish they are just posterior to the pectoral girdle. This general posterior migration has played a part in the lengthening of the esophagus in higher vertebrates.

Organs of the Digestive System

Mouth

The mouth of the chordates appears to be a new structure, not homologous with the mouth of the invertebrates, and there is some difference of opinion as to whether the mouth of the vertebrate is the same as that found in the protochordates. As an entrance way to the digestive system, the mouth is subject to a great deal of variation. In fishes it is closely correlated with water respiration, whereas in tetrapods it is associated with the action of the lungs. The ectodermal lining extends to the region of the pharynx. There are few glands in the mouths of fishes, but there is a progressive increase in these glands, as the land forms become more stable, and the mouth takes a more impor-

• tant part in the preparation of food. The mouth of cyclostomes is jawless and supplied with horny, rasping teeth that aid in their peculiar type of food-getting. The fish mouth is loosely organized and roofed with a number of dermal bones, all of which may bear teeth. The teeth vary greatly, being absent in herbivorous forms and sharp and needle-like in the carnivorous types. Some have crushing plates formed either by the teeth or from the pharyngeal series. Whereas the roof of the mouth is fairly compact, the sides and the floor are likely to be a loose series of bones with a maximum of movement. The large gill slits open into the pharyngeal region, but this gap is guarded by the gill-rakers, which help to direct the food into the esophagus. Numerous deformed fish, in which the mouth has been destroyed by accident, are able to live and maintain a fair metabolic balance. A carp in which the mouth had been completely closed by the bite of some predator (turtle?) was taken from the Illinois River and, although somewhat dwarfed, was in a surprisingly good condition, considering the fact that all the food had to enter by way of the gill slits. Since the food is generally gulped down, no special apparatus for grinding food is needed in the carnivorous fishes. Herbivorous types, however, may have special grinding pads, the carp having a horny pad developed on the basioccipital that works against the large pharyngeal teeth. Similar opposing plates are developed in the pharyngeal series of the fresh-water drum, *Aplodinotus grunniens*. Mouth glands and tongue are of little use in fishes.

The changes foreshadowed by the development of a connection between the nose and the mouth in the Choanichthyes are continued in amphibians and other tetrapods. The amphibian mouth is more compact; even in the urodeles there is a reduction of the gill structure and a closer association of the working parts of the jaws. There is a rapid increase in the number and types of glands, lip, tongue, intermaxillary, choanae, and throat glands being present. Internal choanae are present in the anterior part of the mouth.

The mouth of reptiles is more compact than that of the Amphibia, but there is still some looseness of the skeletal structures. The food is usually gulped and swallowed; the jaws and teeth serve principally for seizing and holding wriggling prey. The entrance of the posterior nares (choanae) is on the roof of the mouth in all but the Crocodilia (Fig. 207) where the palatines and maxillae meet on the midline and force the nares back to the pharyngeal region. This new, secondary roof of the mouth forms the narial passages.

Mouth glands become very prominent and are used primarily for lubrication, with the exception of venom production in the poisonous snakes and in the poisonous lizard, the Gila monster (*Heloderma*). Teeth are present in modern reptiles, except in turtles, which have lost

all signs of teeth and have formed sharp cutting jaws covered with horny epithelium.

The mouth of birds is similar to that of the reptiles in that little action takes place, except for a slight moistening and lubrication of food. The mouth glands are well developed in the grain-eaters and reduced in the carnivorous and water types. No teeth are present in any living bird although fossil forms had reptilian-like teeth. The

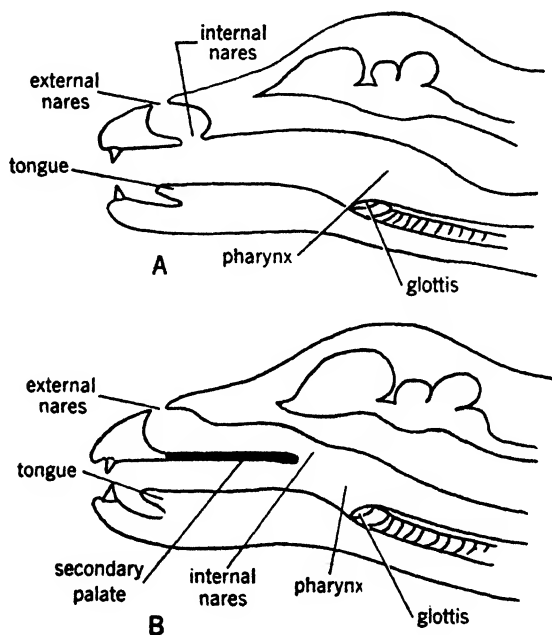


FIG. 207. Diagram showing position of internal nares. A, amphibians and lower reptiles; B, higher reptiles and mammals.

jaws of modern birds are covered with horny epithelium which may be serrated in fish-eating birds. The posterior nares are narrow slits in the roof of the mouth and are not pushed back as in the mammals, because of the failure of the hard palate to meet in the center.

The mammalian mouth has the best separation from the nasal passage (Fig. 207) since the hard palate is well developed and prolonged posteriorly, so that the air enters the pharynx close to the glottis and a smaller area of the alimentary tract is used for air passage. In those mammals in which the food is retained in the mouth and chewed, there is a high specialization of the glands. Some digestion is initiated in the mouth before the food is swallowed. In some, especially in ungulates, the roof of the mouth is cross ridged and covered with horny spines. Highly specialized muscular lips appear outside the jaws.

The teeth are usually diphyodont and show numerous modifications of the mammalian heterodont formula. Certain mammals such as some Cetacea and edentates have become toothless.

Tongue

A structure called a tongue is found in the mouths of nearly all vertebrates. The hagfish (*Myxine*) has a so-called tongue hardly homologous with that of the higher vertebrates. It is covered with horny spines, used to rasp away the flesh of fishes on which they live, and is moved by the musculature of the pharynx and innervated by the hypoglossal nerve. The tongue of fishes is hardly more than a bump on the floor of the mouth and has little function. It may be called a primary tongue. It rests on the midline of the branchial skeleton on the floor of the mouth and extends from the hyoid to the branchial arch, the basibranchial being used as a support. The tongue of tetrapods is a muscular organ formed by the addition of a muscular secondary tongue to the primary tongue. From its position in the mouth, it is probable that it was first used in tetrapods to assist in pushing food back into the pharynx. Highly specialized tongues arise in many of the land-living (terrestrial) vertebrates, where the tongue assumes great importance, not only in handling food in the mouth but also in procuring food. The secondary tongue is generally tactile and may be supplied with taste buds.

In amphibians the tongue varies greatly in size and importance. Amphibians have added the muscular secondary tongue to the primary tongue, and the combination constitutes the tongue of the tetrapods. One group of toads (*Aglossa*) have lost their tongue. Frogs have a highly specialized structure which serves as a means of seizing food and drawing it into the mouth cavity. In the Anura generally the tongue is attached at the anterior end of the jaw and is shot out with great rapidity, catching insects by means of its sticky covering. The muscular system becomes better organized, with a genioglossus as a protractor and a hyoglossus as a retractor, thus giving much more pliability. Its sense organs are innervated by the glossopharyngeal nerve, and its muscles by the hypoglossal nerve.

The tongue in reptiles and birds has several additional parts. The tuberculum impar, a median unpaired tubercle, which originates between the basihyal cartilage and the lower jaw, is added to the median part, and a fold is added to each side. A branch of the trigeminus serves these additional parts, so that three cranial nerves are concerned in the innervation of the tongue. In lizards and snakes the tongue is highly protractile and is often used for food-getting. It is bifid in many lizards and in all snakes. In turtles and crocodiles the

tongue is broad. Crocodiles have transverse folds on the posterior portion of the tongue, and a palate which can be used to close the pharynx and separate it from the mouth. The skeletal parts consist of the modified visceral skeleton, the hyoid bones, which are used as a tongue support and generally consist of a median element and two cornua, or horns. In woodpeckers the cornua are curved over the skull, ending at the nostrils, and are enclosed in a synovial sheath that permits free movement, so that the tongue can be protruded astonishingly far. The tongue of birds is often covered with horny papillae, those of the woodpeckers being barbed.

The most complex type of tongue appears in the mammals, where it is in constant use in grasping food, pulling it into the mouth, and moving the bolus, or ball of food, from side to side in mastication. It also assists in swallowing and, of course, aids speech in man. The mammalian tongue seems to be formed by an additional structure superimposed upon the reptilian tongue, although this may be disputed. The basal region, or sublingua, probably is the same as that of reptiles and birds; the fleshy region is peculiar to the mammals. This part of the tongue consists largely of interlaced muscles, which make it capable of versatile movements. The tongue is supplied with a series of sensory structures principally concerned in taste and in touch. The taste buds are usually near the base of the tongue and around the circumvallate papillae. Each bud, or bulb, consists of taste cells, which are depressed below the surface and open by small orifices. They detect only materials in solution. Small papillae, shaped like small mushrooms, are scattered over the tongue in irregular areas. Carnivora and ungulates may have horny papillae which assist in holding and may be used in rasping. The tongue is richly supplied with blood vessels and lymph nodes. A watery mucous secretion is supplied by other glands on the surface. Three nerves are concerned in the innervation, the trigeminus, glossopharyngeal, and vagus.

Glands of the Mouth

The glands of the mouth are a development of land life, being absent in all but a few water forms. Animals that have returned to the water, such as turtles, water birds, cetaceans, and water mammals, have either lost the glands or have them greatly reduced. Fish generally lack mouth glands, whereas the glands of the amphibians are few in number and are located on the roof of the mouth or on the tongue.

A number of large salivary glands appears in the higher vertebrates. Reptiles show a very great development of the palatine, sublingual, premaxillary, and labial glands. The superior labials (Fig. 195) of the

poisonous snakes and the lower labials of *Heloderma* produce venom. The mouth glands are generally little developed in birds, except at the corners of the mouth, but they reach their highest development in mammals where they supply three kinds of secretions: mucus, a relatively heavy lubricant; a serous fluid, a thin lubricant; and ptyalin, a digestive enzyme that acts upon starches. Recent work has demonstrated that the submaxillary glands of the short-tailed shrew, *Blarina*, secrete a substance remarkably like snake venom in its action on

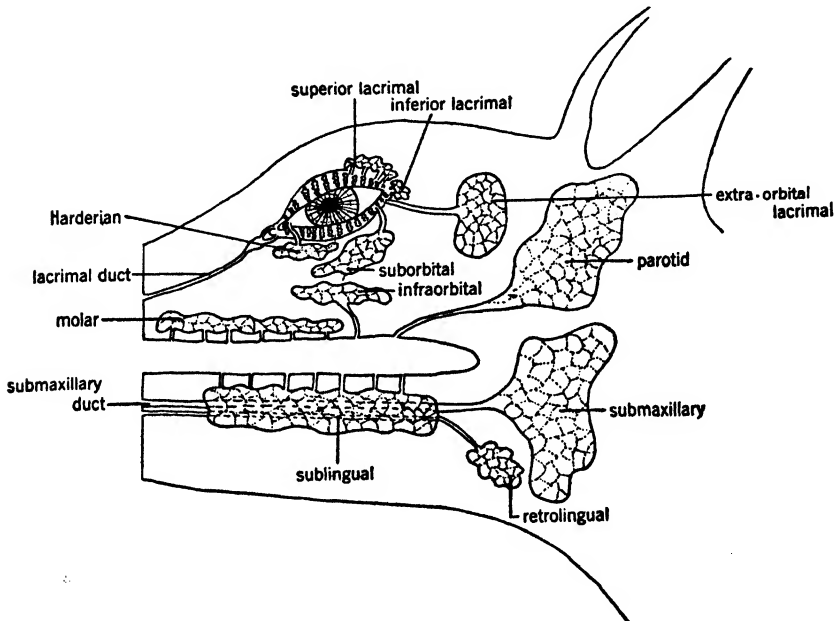


FIG. 208. Diagrammatic arrangement of the salivary and lacrimal glands of mammal. Redrawn from Plate and Weber.

warm-blooded animals. The labials, palatines, and buccals (modified labials) suggest the glands of the skin in their structure. The linguals, sublinguals, and retrolinguals pour their secretions into the mouth along the borders of the tongue (Fig. 208). The parotids, the largest mouth glands of the mammal, are ventral to the ear, at the angle of the jaw, and send their secretion into the mouth through the sides of the cheek by means of the parotid ducts. The submaxillaries are quite large and very much in evidence on the medial line of the throat, at the angle of the jaws. The submaxillary ducts (Wharton's) open under the tongue to the anterior part of the mouth. Ungulates have large molar glands that pour a copious supply of watery secretion over dry food. In cetaceans and sirenians, which are strictly aquatic,

the mouth glands are reduced almost to vestiges, but in the pinnipeds (seals) these glands are fully developed.

Pharynx

The pharynx, being concerned with the respiration as well as digestion, exhibits more modifications than any other part of the digestive system. Its walls are broken through in the fishes by the gill slits. These openings are universal in the fishes and retained in the adults of some amphibians. The posterior nares of the tetrapods, originally opening into the anterior part of the mouth, become forced back to the pharynx by the formation of a secondary roof, the hard palate in the higher reptiles (Crocodilia), and this condition is typical of the mammals. The first pair of gill slits is retained in all vertebrates above the fishes as the Eustachean tubes. These tubes open as two apertures into the pharynx of tetrapods, although they may have a common opening in birds. In fishes the duct from the swim bladder generally opens into the pharynx (Fig. 209 *B, C*), though sometimes into the esophagus or even into the stomach. The trachea of the lungs of land vertebrates open into the floor of the pharynx through a slit known as the glottis, which has a protecting flap, the epiglottis, in mammals. From the floor originate a number of glands, including the thyroids, parathyroids, and the thymus. The pharyngeal tonsils, parathyroids, and thymus are derived from embryonic gill pouches.

Tonsils

Several tonsil-like structures composed of lymphoid tissue appear in the vertebrates. Fishes and amphibians have lymphoid glands in the pharyngeal region that, perhaps, have some relation to the tonsils of the higher vertebrates. Reptiles and birds have well-defined pharyngeal tonsils that also appear in some mammals. The pharyngeal tonsils of the amphibians, reptiles, and birds are on the roof of the posterior choanae; the palatine tonsils, characteristic of mammals, are on the lateral side of the pharynx. The lingual and palatine tonsils are characteristic of the mammals and are quite consistent in their appearance. The lingual tonsils are small isolated, lymphatic structures that appear at the base of the tongue, consisting of a small pit, lymphatic nodules, and a small opening to the surface. They have the structure of a small palatine tonsil. The palatine tonsils are stable structures of the mammals and one of their characteristics. This tonsil originates from the pharyngeal region of the second gill pouch, starting as a small pit lined with mucous membrane that later forms simple folds. The folds may be complicated by the formation of a branching system for each fold. The tonsil is made up of a connective tissue

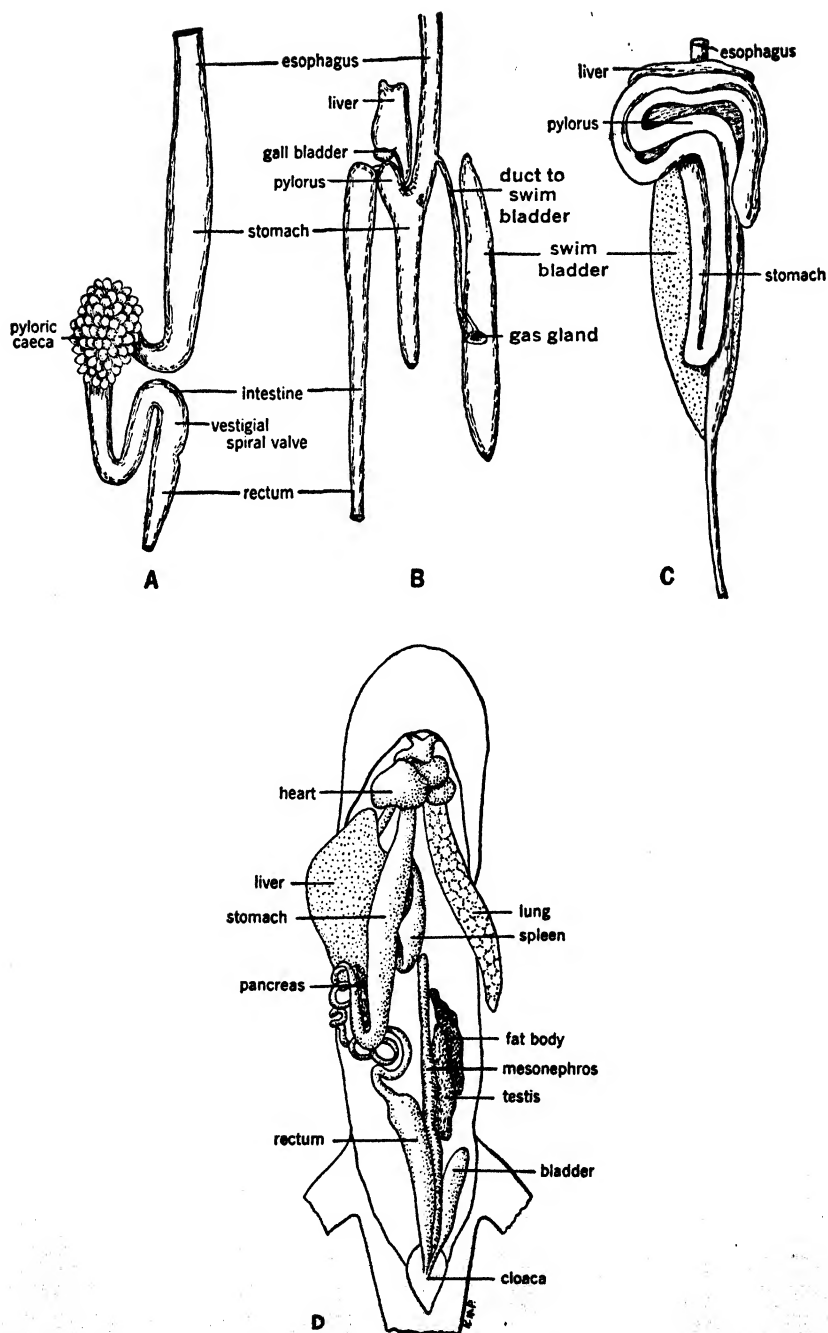


FIG. 209. Digestive systems of fishes. A, *Lepisosteus*; B, eel (*Anguilla chrysopa*); C, sucker (*Catostoma commersonii*); D, viscera of *Ambystoma*.

capsule that partly surrounds it, folded mucous membranes covering large lymph nodules (adenoid tissue), and an opening to the throat. The tonsils of man have a rather complicated series of crypts and a single opening to the throat.

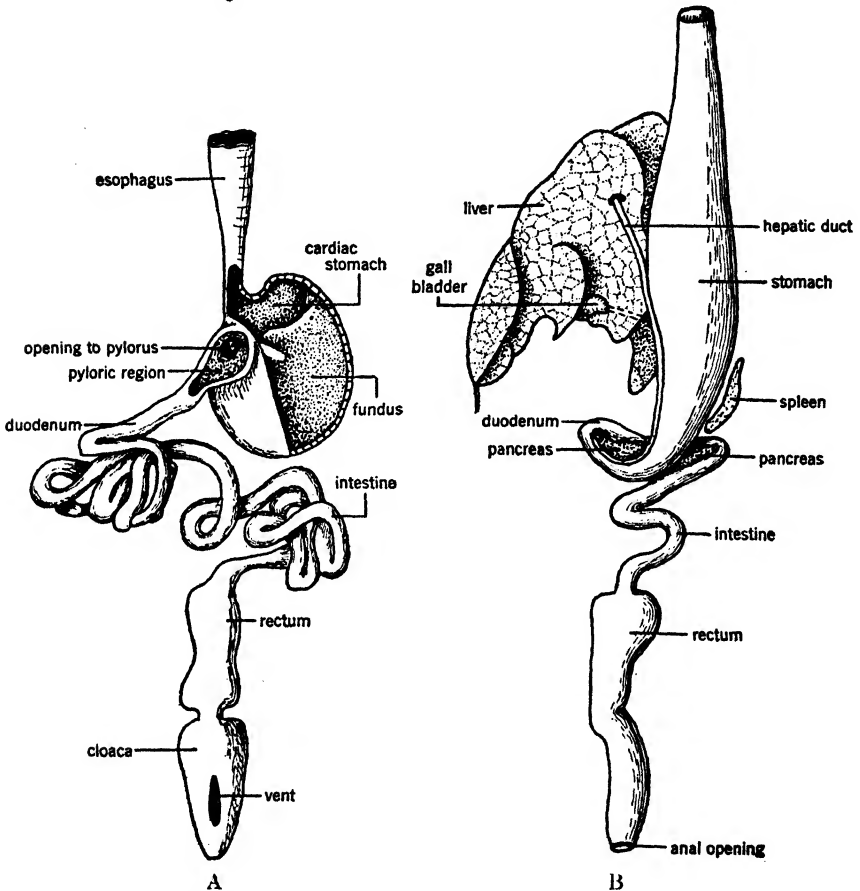


FIG. 210. Digestive systems of reptiles. A, alligator, B, *Sceloporus*.

Esophagus

The digestive tube proper starts with the esophagus, which is little modified, being simply a passageway from the pharynx to the stomach. In structure it resembles the rest of the digestive tube, in that it is composed of mucosa, submucosa, and muscular layers (Fig. 216) but the serosa is lacking. Its function is to pass the bolus of food along to the stomach and supply enough glandular secretion for lubrication only, since the food ordinarily remains in it only a short time. Cyclostomes have little differentiation of the foregut, and it is rather difficult

to draw a line between the stomach and the esophagus. Fishes also have little differentiation between the esophagus and the stomach, the principal difference lying in the glands and their distribution. A few fishes, such as the eels and some of the elongated forms, have quite a clear distinction. The tube is often smooth, may be slightly folded, or may have papillae as in *Squalus* and *Acipenser*. Amphibians generally have a short undifferentiated esophagus, except in the elongated forms such as *Siren* and *Amphiuma*.

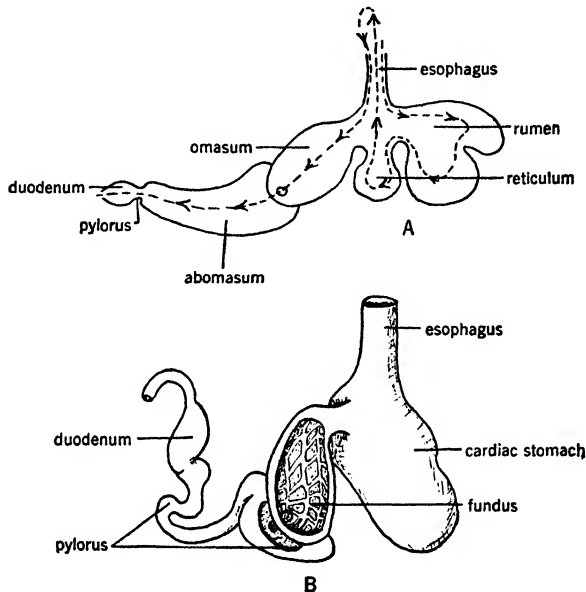


FIG. 211. Mammalian stomachs. A, the stomach of a ruminant showing the pathway of food through the divisions. After Kingsley. B, stomach of a seal. After Bütschli.

With the development of the neck and the posterior migration of the heart and stomach in higher tetrapods, the esophagus lengthens appreciably. It becomes much better differentiated from the stomach in reptiles and may be lined with horny papillae as in turtles. Birds present some modifications partly because of the elongated necks found in this class. They modify the esophagus forming an enlargement, the crop, which is used for the storage of food in most birds. The epithelium of the crop of pigeons and some other birds proliferates a substance called "pigeon's milk," which is fed to nestlings. Mammals have a definite esophagus usually distinct from the stomach, although in some animals the line of demarcation is not very clear. The rumen and reticulum, the first two compartments of the sheep stomach, are really a modified part of the esophagus (Fig. 211 A).

Stomach

The stomach is a division of the digestive tube differentiated for food storage and the preliminary stages of digestion. It supplies digestive juices to the food and gets it in a proper condition for action by the small intestine. It has a gentle motion that agitates the food and mixes it with the secretions of glands in its walls, which are incited to act by hormones or by the food itself. The stomach is held in place by the mesogaster (Fig. 205), a part of the dorsal mesentery which suspends it from the posterior wall of the coelom. It is divided into several regions, each characterized by the presence of glands of a certain type: the cardiac region, into which the food first goes, supplies

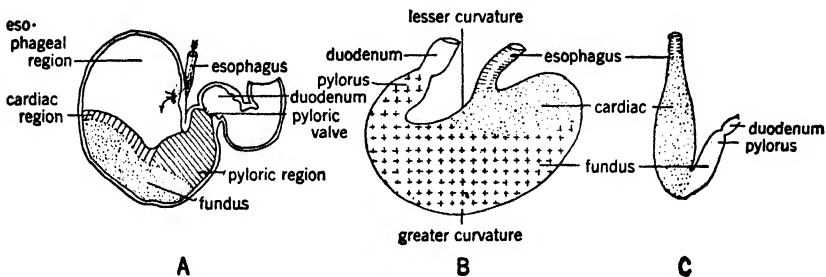


FIG. 212. Mammalian stomachs. *A*, stomach of horse. After Sisson. *B*, stomach of a rodent; *C*, stomach of a seal. After Weber.

an albuminous fluid; the fundus, or mid-region, supplies the gastric juice proper; the pylorus, or third region, adds mucus to the digesting materials (Fig. 212). The pyloric region is separated from the duodenum by a sphincter muscle, which permits small quantities of the stomach contents to pass when they are in a proper condition and have reached a definite stage of acidity.

The stomach in vertebrates generally is well supplied with blood vessels and lymphatics and is innervated by the autonomic system (coeliac plexus) and vagus nerve.

The stomach of the fish and the amphibian is comparatively simple and little differentiated from the rest of the gut. In these lower vertebrates the stomach is either a straight sac-like tube or it may be bent in a J-shape. Some primitive bony fishes and teleosts develop caeca at the pylorus. These are finger-like pockets ranging in number from one to several hundred. Many reptiles retain a simple stomach although some fossil dinosaurs had a gizzard. Modern crocodiles have a heavy muscular, gizzard-like development of the cardiac portion.

The stomach of birds (Fig. 213) is composed of the proventriculus and the gizzard. The proventriculus, not much larger in diameter than

the esophagus, is supplied with the glands usually found in the anterior part of the stomach, which pour their secretions over the food material and soften it. The gizzard is best developed in grain-eating birds. It is highly muscular with heavy walls and a horny lining. The horny pads, together with swallowed stones always found in this organ, form a grinding mill, capable of reducing hard grains to a paste. The exit of food through the pylorus is close to the entrance from the proventriculus.

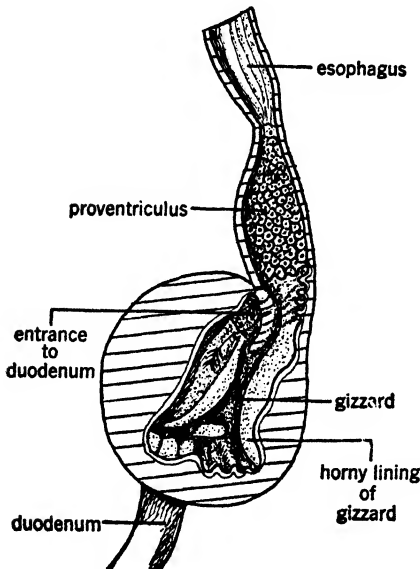


FIG. 213. Stomach of sparrow (*Passer domesticus*), sagittal section.

The mammalian stomach is variable in shape, differing greatly in the various classes. Typically there is a greater curvature extending around the long side and a lesser curvature along the short side. The inside is folded so that the lining appears to be wrinkled. Besides the four layers of the esophagus, a fifth layer, the serosa, is added. In mammals the stomach is usually a single chamber, but it may consist of as many as four in some ungulates. In sheep (Fig. 211 A), for example, the first two chambers (rumen and reticulum) are developments from the esophagus, and the last two chambers (psaltarium and abomasum) constitute the "true" stomach. The

food, when partly chewed, passes down the esophagus into the large paunch, or rumen, which serves as a storage chamber. From this it goes into the reticulum, a small chamber with honeycombed walls, which rolls it into a ball, or cud, ready for regurgitation and mastication. On being swallowed the second time, it goes to the third chamber, the psaltarium, or omasum, which mixes it with gastric juices, and thence to the fourth chamber, the abomasum, where the preliminary stages of digestion are continued until the food is in proper condition to pass through the pylorus into the small intestine. In one of the bats, a caecum is developed from the fundus, and in the hippopotamus a pair of caeca are developed from the same region.

Intestine

The intestine, with its divisions, carries on the process of digestion and rejects the waste products as feces. Starting with a straight tube

in lower vertebrates, it becomes lengthened, folded, and specialized, increasing the area for absorption roughly in proportion to the bulk of the animal. The proportion is maintained by folding the inner surface, increasing the length, and developing spiral valves and side pouches, or caeca.

The intestine was probably first a more or less straight undifferentiated tube as seen in the cyclostomes. However, fishes modified it rather early. Sharks (Fig. 214) and a few primitive fishes, such as the sturgeons and *Polyodon*, developed the major part of the intestine into a spiral valve arrangement (Fig. 215 A) increasing the surface about three times. The intestinal structures of such fishes are hard to homologize with intestinal structures of higher vertebrates. The intestine starts at the pyloric valve of the stomach and forms a tubular duodenal area receiving the bile and pancreatic ducts. Then comes the swollen spiral-valve part often called the ileum. This is followed by the rectal region or colon emptying into the cloaca. A rectal gland, a caecum, is located about midway on the rectum and probably secretes mucus.

Teleost fishes have developed the coiled, tubular type of intestine which may be almost straight in the herring (*Clupea*) or much coiled as in some minnows. The pyloric caeca, already mentioned, are prominent at the anterior end of the intestine. No differentiation of the colon or large intestine from the small intestine occurs in the teleosts. Amphibians, reptiles, and birds likewise have this coiled, tubular type of intestine, modified posteriorly by the development of the colon. In these forms the colon is short and does not reach the size found in mammals. It will be discussed later.

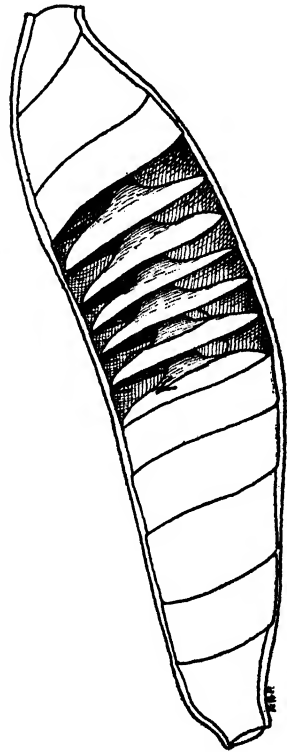


FIG. 214. The ileum or spiral valve of the shark, *Squalus acanthias*.

Small Intestine of Mammals

In the mammals the small intestine is divided into three regions, the duodenum, jejunum, and ileum. The duodenum starts at the pyloric valve and ends beyond the entrance of the ducts from the liver and pancreas. The duodenum supplies a hormone, secretin, which

enters the blood and causes the pancreas to release its juices. The remainder of the intestine is somewhat arbitrarily divided into jejunum and ileum. The jejunum, forming about two-fifths of the remaining intestine, receives the food material from the duodenum, and here the process of digestion is completed by the addition of the succus entericus, or intestinal juice, and absorption takes place.

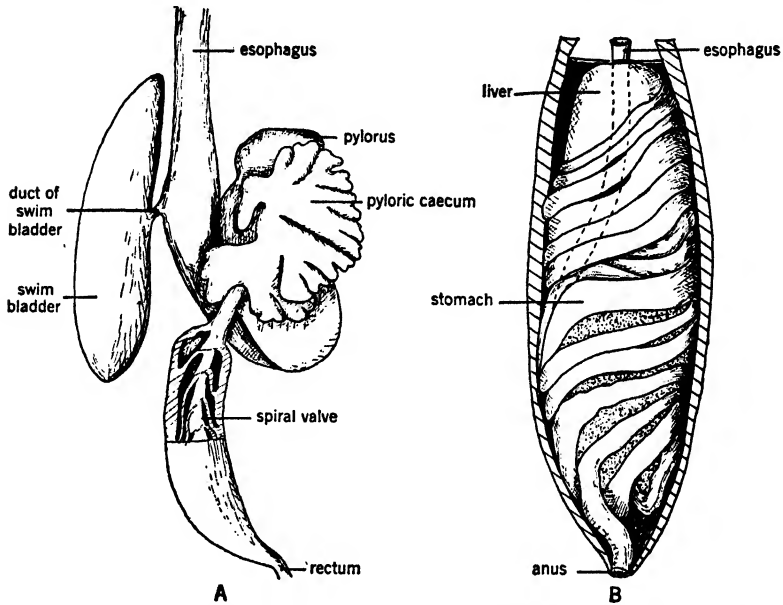


FIG. 215. A, Digestive system of the paddlefish (*Polyodon spathula*), showing large and peculiar caecum. B, Digestive system of the stone-roller (*Campostoma anomalum*), in which the intestine is wound around the swim bladder.

The lining of the jejunum is thrown into concentric folds or ridges, called plicae circulares, by thickenings of the mucosa and submucosa, and on these ridges are placed the villi, small finger-like processes that select and absorb the digested food. These ridges disappear in the ileum. The villi cover the inner surface of the small intestine giving it a soft, velvet-like appearance. Each villus is made up of a small artery and vein, a nerve, and lymph vessels. The glands of Lieberkühn, which supply the succus entericus, have their openings at the bases of the villi. The small intestine is richly supplied with blood vessels, and it is here that the process of absorption is carried on. Food enters the blood stream through these villi, being taken into the veins and thence through the connecting vessels to the hepatic portal and the liver. Fats are absorbed by the lymphatic system of the villi, and going through the lacteals of the mesenteries, reach the venous system, anterior to the heart, through the thoracic ducts. (Fig. 216.)

Lymph vessels and structures are associated with all digestive tubes, but they become prominent in the reptiles and continue through to the mammals, where they form large aggregates in the walls of the digestive system. They may be simple follicles scattered along the tube, or they may be collected into aggregates or patches, as in the mammals, where they form the Peyer's patches. These patches of follicles are most plentiful in the small intestine, although they may extend into the colon. In the human intestine these patches may be half an inch wide

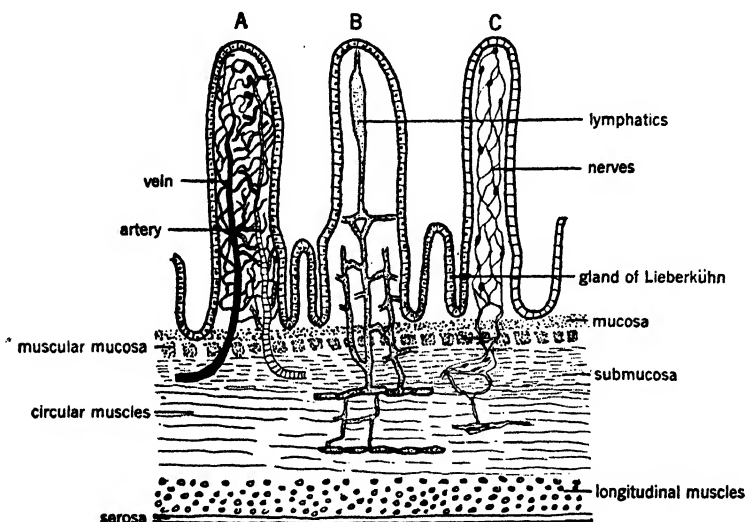


FIG. 216. Diagrammatic drawing of the villi of the intestine. *A*, blood vessels of the villus; *B*, chyle vessels; *C*, nerve net. Modified from Mall.

and three or four inches long. They occur on the wall of the intestine, opposite to the attachment of the mesenteries. They appear as raised areas and are quite distinct. Prominent in young animals, they become less conspicuous with age. In typhoid fever, these patches are broken down by the action of the bacteria so that the intestinal wall is perforated.

The rhythmic action of the longitudinal and circular muscles, which are controlled by the autonomic system, causes a gentle peristaltic movement that advances the food slowly through the entire digestive tube.

Colon

The lower end of the intestine becomes enlarged to form a colon in the higher vertebrates. The colon appears in the amphibians and is also present in the reptiles as a short enlarged portion opening into

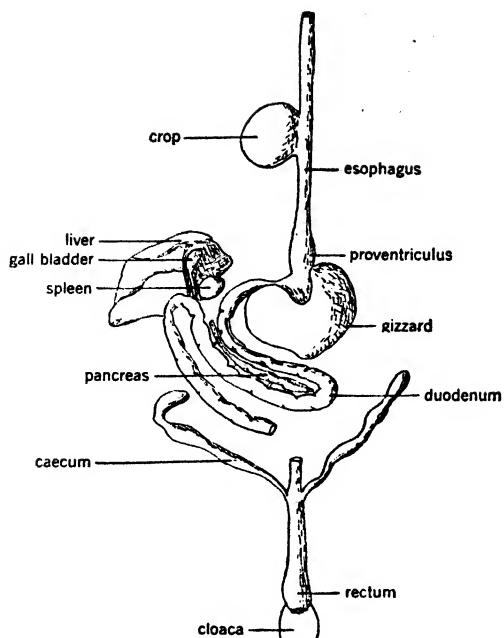


FIG. 217. Digestive system of chicken.

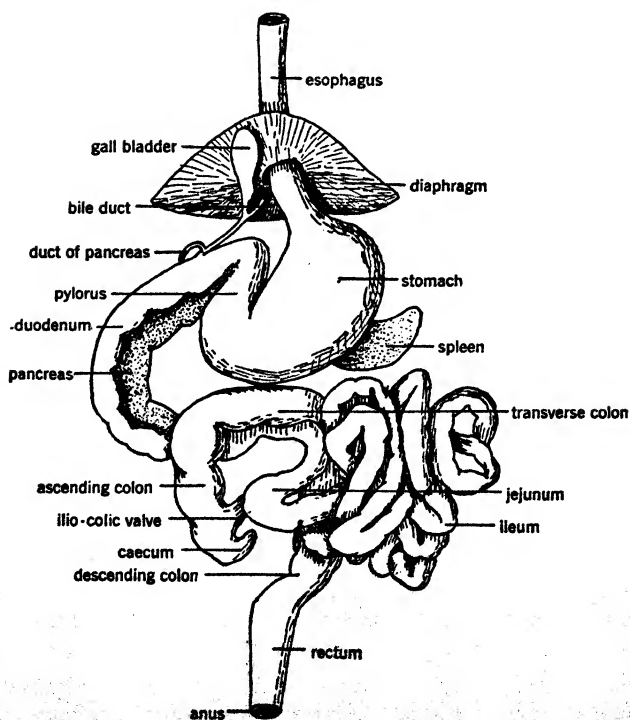


FIG. 218. Digestive system of the cat (liver removed). After Davidson.

the cloaca. Birds have a short colon, usually characterized by a pair of large caeca on the anterior end (Fig. 217). Birds have a gland, the bursa of Fabricius, of problematic function on the dorsal posterior wall. This is often lost in adolescence.

In mammals the small intestine enters the colon rather abruptly and often at right angles (Fig. 218). The colon of many mammals originates in a blind caecum, which may be as large as the stomach in rodents (Fig. 219) or merely a blind end of the colon as in carnivores. In the human, the caecum is vestigial and ends in the vermiform appendix which is a vestige of an extension of the caecum.

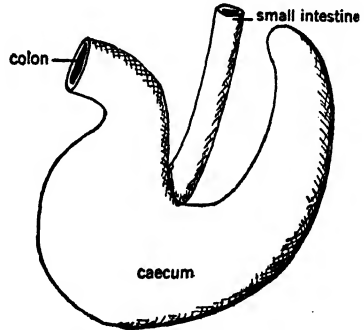


FIG. 219. Caecum of intestine of white rat.

The mammalian colon originates on the right side of the abdomen, usually ascends anteriorly a short distance, and passes transversely to the left, then descends posteriorly to the anus. The posterior portion just before the anus is the rectum. The colon is large, particularly in mammals feeding on fibrous vegetable matter. It may be somewhat coiled, although in some, as in the cat, it is without coils.

Most of the absorption has taken place by the time the food reaches the large intestine, and this distal end of the digestive tube serves to

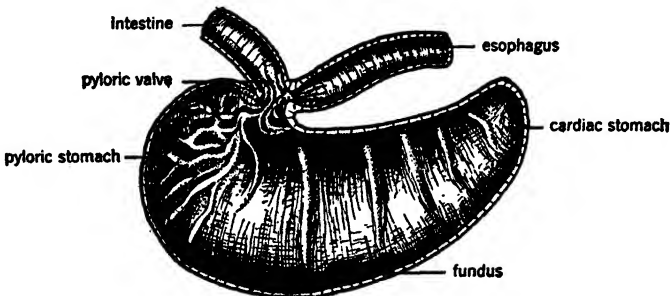


FIG. 220. Stomach of white rat.

reduce the bulk of the feces by extracting the water. In animals eating large amounts of cellulose, some reduction and digestion may take place, usually by bacterial action. The villi generally disappear at the beginning of the large intestine, or at most extend but a short distance along its length. Its surface is not so much folded, and the plicae circulares disappear. Lymph nodules are found in the tube, but no

structures resembling Peyer's patches. Its juices are supplied by mucous glands whose general function is to supply lubrication.

The rectum (Figs. 210, 218), is a relatively short, thick-walled region at the distal end of the colon, concerned in the expulsion of the feces. The anus, or outlet, is protected by sphincter muscles, which in the higher animals are innervated by both the autonomic and voluntary systems.

Cloaca

Many of the vertebrates have a cloaca or common chamber into which the digestive and urogenital systems discharge (Figs. 209, 210, 217). Ordinarily the cloaca is divided by a fold into two parts, the coprodaeum into which the intestine empties and the urodaeum into which the urogenital ducts empty. The external opening of the cloaca is the vent, often called the anus. The anus properly refers to the opening of the digestive tract and, consequently, in those forms with a cloaca, should apply to the opening of the intestine into the cloaca. The cloaca is absent in the Holocephali, ganoids, teleosts, and the higher mammals. Monotremes possess a shallow but definite cloaca. It has flattened out still further in the marsupials and appears only as a shallow depression containing the anus and the urogenital apertures. In the placental mammals the cloaca has disappeared except in the embryo, although in some the urogenital apertures still occupy a common depression. In vertebrates below the mammals the cloaca may have pouches for the storage of urine.

The Liver

The liver, the largest gland of the body, occurs in all vertebrates. Originally it was on the walls of the intestine, but it has pulled away and now is connected only by ducts. In structure it is a tubular gland that has masked its appearance by overgrowth. In ancient days it was regarded merely as packing for the rest of the organs, but now it is recognized as important, not only in digestion, but also in the general body metabolism.

The shape of the liver varies with the body of the animal, being short or long according to the body form. It is generally divided into two unequal parts, each with a varying number of lobes (Fig. 221). It is covered with a part of the serosa, which follows it in its development. It is attached by the coronary ligament to the transverse septum (diaphragm in mammal) and by the falciform ligament to the ventral body wall. The texture of the liver is such that it is easily ruptured, since it has little connective tissue in its structure and its serosa offers

only a slight protection. The internal structure of the liver consists of units of polygonal cells, forming a lobule (Fig. 222) similar to a tubular gland. These units are surrounded by capillaries.

The tissue of the liver (Fig. 222) itself is supplied by the hepatic artery. The venous blood from the digestive tube is carried to the

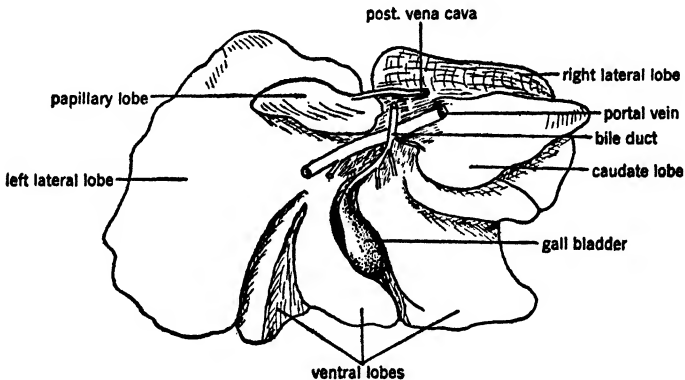


FIG. 221. Liver of the dog. After Sisson.

liver by the hepatic-portal vein, which delivers it to the capillaries of the individual lobules, where it is exposed to the action of the cells of the lobule. Along these capillaries are the fine, interlacing bile ducts which collect the bile and carry it to the hepatic duct and to the gall bladder. The gall bladder, an enlargement extending off from the bile duct, stores bile. It occurs in all groups of vertebrates above the cyclostomes. It may be absent entirely in some birds and mammals. The common bile duct, or choledochal duct, carries the bile from the hepatic and cystic ducts to the intestine, discharging it through the influence either of a hormone or of the fats in the food. The liver is innervated by branches from the vagus nerve and also from the coeliac plexus of the autonomic system.

Besides supplying the bile for the digestion of fats, and for lubrication, the liver stores glycogen. Urea and uric acid, formed in the liver from the ammonia compounds of the blood, are sent to the kidneys

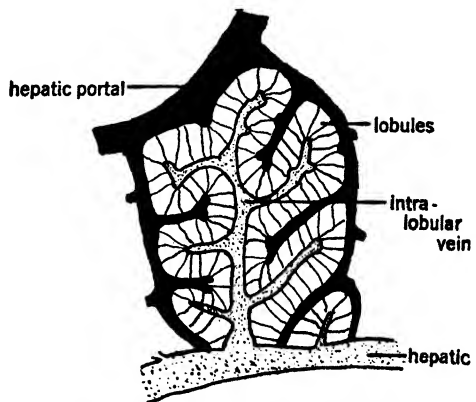


FIG. 222. Section of liver. After Weber.

for removal. Old and worn-out erythrocytes are also removed from the blood stream by the liver.

Pancreas

The pancreas, a companion gland to the liver, is a marvelous chemical laboratory in a small space and one of the most important glands of the body. It takes its origin, as does the liver, from the walls of the digestive tube and is a constant structure in all vertebrates. (Figs. 210, 217, 218.) Originating from two or more diverticula, it becomes consolidated to form one gland with several ducts, usually a main pancreatic duct (duct of Wirsung) and an accessory duct (duct of Santorini), although more ducts may be present or a single duct may function alone. Frequently the ducts join those of the liver and enter the duodenum through a common duct. Its position is always close to the intestine, and it often follows a fold so that it becomes a U-shaped organ. Its structure is that of an acinose gland. The pancreatic juice, incited to flow by the secretin from the duodenum, which reaches it through the blood stream, supplies all the enzymes necessary to complete the digestive processes. Its removal causes death to the animal. The islets of Langerhans, in the tissue of the pancreas, supply a hormone that is very essential in the control of the amount of sugar in the blood. This hormone, isolated by Banting and Best in 1921, was named insulin and is now used all over the world for the control of diabetes.

The digestive system, though performing some of the most complicated chemical processes, undergoes no radical changes from the lowest to the highest vertebrates. As the requirements of digestion are much the same in all vertebrates, as far as the main features are concerned, the greatest variations and improvements come in meeting the conditions imposed by different foods and in maintaining the area of the digestive tube in proper proportion to the bulk of the body.

CHAPTER TWELVE

Circulatory System

A vascular or circulatory system through which blood circulates is found in all vertebrates, and, throughout the subphylum, both the vascular pattern and the characteristics of the circulatory medium are remarkably constant.

The circulatory system consists of the heart, which is a central force-pump; the veins, which carry blood to the heart; the arteries, which take it away; and the capillaries, which connect the arterial and venous systems. The veins are thin-walled and have pocket valves at intervals; the arteries have much thicker and stronger walls. Smooth muscle tissue in the walls connected with the autonomic system, makes possible the dilation and constriction of both systems. The lymphatic system is an important link in the circulation, since it returns the plasma that has escaped from the vessels into the tissues. (Fig. 263.)

The circulation problem concerns all living things, since there must be ways for transporting materials to and from all parts of the living structure. This transportation is rather simple in the lower animals, but it becomes very complex with higher organization and with types of covering that are more impervious and prevent an interchange of gases. As these coverings develop, definite areas are established for oxygenation, taking away waste, and adding food materials. Definite, closed systems do not usually occur below the vertebrates, for the lower animals have less definite vessels, with lacunae or open spaces in which the circulating fluid can collect.

Blood

For convenience the blood can be considered as a fluid (plasma) in which some substances are dissolved and in which the red blood cells (erythrocytes), white blood cells (leucocytes), and other materials are suspended. The plasma is a straw-colored fluid containing: water; food; waste; salts; enzymes; products of the ductless glands, or hormones; materials concerned with immunity and toleration of disease germs, toxins and antitoxins. The plasma also contains fibrinogen, a substance which forms threads and thus assists in the formation of

clots when the blood is exposed to air or to foreign structures or materials. Clotting is further aided in mammals by the small platelets which disintegrate rapidly in exposed blood. An adult human has about one gallon of blood, and each cubic centimeter contains from four and a half to five million erythrocytes and from five to seven thousand leucocytes.

The red corpuscles, or erythrocytes, found in all vertebrates but absent in all other animals, are small cells, concerned principally with carrying oxygen to the tissues. They contain hemoglobin, which has the power to take up large quantities of oxygen, and in this way oxygen is carried to different parts of the body and released. Erythrocytes do not appear in the blood of *Amphioxus*. In the lower vertebrates, they are large, more or less oval, and have a distinct nucleus. Mammals, with the exception of the camels, are unique in having small concave disc-like erythrocytes which, when mature, have no nuclei. Consequently the red corpuscles are short lived, lasting only about a month. A continuous supply is made in the several blood-forming organs. The erythrocytes never leave the arteries, veins, and capillaries. The largest red corpuscles are those of the amphibians, which are from five to ten times larger than those of man. The smallest are said to be those of the musk deer.

The leucocytes, or white corpuscles, are ameboid in shape and are larger than the red. They are able to leave the veins and arteries through the walls of the capillaries and get into the tissues and the lymph stream. They have the ability to move with an ameboid movement. They are differentiated into several types with quite different functions. They carry materials from place to place in the body, remove dead cells, combat bacteria and other parasites that find their way into the blood stream, and act as guardians of the circulatory system generally. Leucocytes are formed in the lymphoid tissues and red bone marrow and added to the system.

Origin of Blood

In the embryo, blood arises from patches of mesenchyme cells, but, after the organs appear, blood cells arise in the spleen and the marrow of the long bones. The spleen in the lowest vertebrates appears as tissue in the wall of the digestive tract. In cyclostomes, splenic tissue occurs in the submucosa of the stomach and intestine. In elasmobranchs and all higher vertebrates, except the Dipnoi, the spleen has pushed out as a separate organ in a mesenteric fold attached to the stomach. In the Dipnoi it remains in the stomach wall. In the higher vertebrates beginning with the Anura, marrow appears in the long bones and takes over much of the function of blood formation.

Functions of Blood

The functions of the blood are numerous and complicated. The food supply from the digestive tract is carried to the cells by the blood; water and oxygen are carried to the tissues and liberated; and hormones and enzymes are carried to the place where they are needed. The removal of waste is accomplished as the blood circulates around the body. Waste materials are taken into the stream to be disposed of at special points, and carbon dioxide is collected and taken to the lungs where it is removed. The lungs enable the blood to get a new charge of oxygen after discharging the carbon dioxide. Nitrogenous and other wastes are removed by the kidneys, and the skin removes some surplus water and salts. The liver removes worn-out erythrocytes and stores surplus food materials not needed at the time. In the regulation of temperature, one of the important functions in birds and mammals, the circulatory system is linked with the autonomic nervous system, which regulates the supply of blood to outer or inner tissues.

Heart

The circulatory systems of the lower chordates are of the invertebrate type; only the cephalochordates approach the vertebrate type. *Amphioxus* has a fairly well-defined circulatory system in which the vessels are well established, with dorsal and ventral vessels and a hepatic portal system. No definite heart is present, although some consider the vessel carrying blood to the gills to be a valveless, single-chambered heart. Others have identified a vessel which they consider a primitive sinus venosus. The blood is directed forward to the gills, principally because of mechanical features that prevent it from moving backwards through the capillaries of the liver. A large dorsal vessel, recognized as the dorsal aorta, carries the blood from the gills posteriorly. The blood is colorless and lacks erythrocytes.

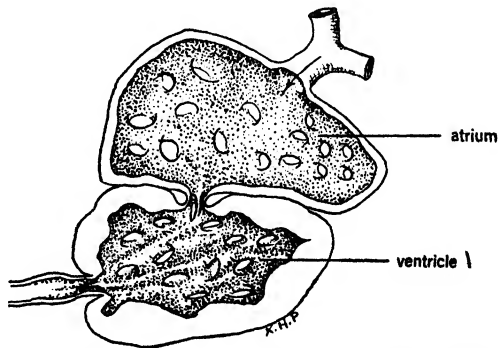


FIG. 223. Section of heart of *Ichthyomyzon unicuspis*, silver lamprey.

The heart probably made its appearance in the earliest vertebrate. The most primitive vertebrate heart known is in the cyclostomes (Fig. 223), where it has already assumed the basic plan characteristic of

all vertebrates. In basic plan the heart consists of two major chambers, a muscular receiving chamber, the atrium, and a heavy muscular pumping chamber, the ventricle. Two accessory chambers are also present: the sinus venosus, emptying the blood from the veins into

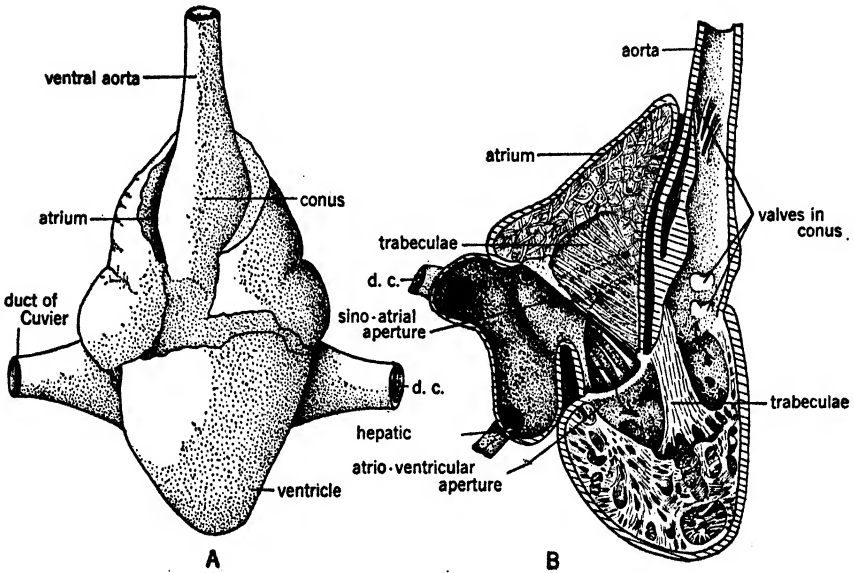


FIG. 224. Heart of *Amia*. A, ventral; B, sagittal section.

the atrium; and a conus, receiving blood from the ventricle and discharging into the aorta. These become more or less obliterated in the higher vertebrates. Fishes retain the two-chambered plan, but the higher vertebrates divide the chambers, forming so-called three- and

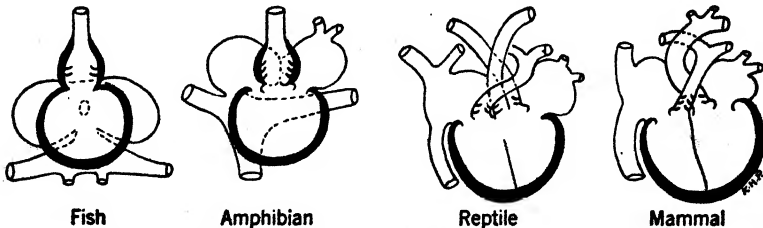


FIG. 225. Diagram showing changes in the heart of vertebrates.

four-chambered hearts. It is three-chambered in amphibians and four-chambered in birds and mammals. It is equipped with valves, so that the blood once started through cannot return to the chamber from which it was forced.

The heart is enclosed in a special pericardial cavity, surrounded by a pericardial sac, and immersed in a serous fluid which supplies the necessary lubrication. The epicardium, a smooth layer of mesodermic tissue, covers the heart, and the endocardium lines it.

Embryology of the Heart

The heart is really a specialized portion of an embryonic blood vessel, which becomes S-shape and forms chambers. In the embryo, the heart originates from vessels ventral to the pharynx. Usually two vessels arise in the ventral mesentery and fuse, and from them the heart tissue differentiates. The vessels form from mesenchyme and soon establish connections. At first the heart is tubular, with veins entering posteriorly and the artery leaving anteriorly. The ventral aorta passes forward to the aortic arches which empty into the dorsal aorta. The dorsal aorta arises as a paired vessel and soon fuses into a single vessel. A transverse septum soon forms posterior to the heart, cutting it off from the rest of the cavity of the hypomere.

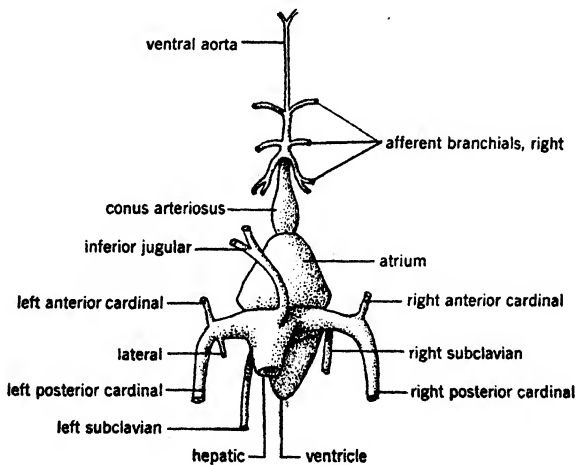


FIG. 226. Heart of *Lepisosteus*, dorsal. After Schimkewitsch.

Position of the Heart

The relation of the heart to the head region undergoes a continuous change from fishes to mammals. In fishes and amphibians, the heart is immediately posterior to the head and in close connection with the gills, which naturally have a decided influence on its position. There is a slight retraction in the amphibians, but the heart is still well forward. In amniotes, however, there is a gradual shift to the posterior with the development of the lungs and the elongation of the neck, so that the

heart moves backward (Fig. 206) and carries with it the elongated blood vessels of the carotid and jugular system.

Heart of Cyclostomes

The cyclostomes, or lowest living vertebrates, have a well-established circulatory system that is both primitive and specialized. The heart has two chambers (Fig. 223), an atrium and ventricle, both with a pair of valves. A small conus is present at the beginning of the ventral aorta. The specialization is noticed in the loss of the left Cuvierian duct in *Petromyzon*. The blood of the cyclostomes is red and has both types of corpuscles.

Heart of Fishes

The two-chambered heart of the fishes has the rather simple duty of pushing the blood from the body through the gills, with no return to the heart itself until the circuit is completed. The position of the heart is just posterior to the visceral arches and very close to the gills. Only two chambers, the thin-walled atrium and the muscular ventricle, are necessary for this operation. The heart of a fish includes a thin-walled accessory chamber, the sinus venosus, which collects the returning blood from the ducts of Cuvier and the hepatic veins and delivers it to the atrium. A membranous partition makes a partial separation of the sinus and the atrium. The connecting aperture is guarded by valves. The passage of the blood from the atrium to the ventricle is almost mechanical: the atrium is directly over the ventricle, so that a gentle pressure drops it into the ventricular chamber. A pair of flaps serves as an atrio-ventricular valve between these two chambers. As the blood leaves the heart, it enters the conus arteriosus, a muscular structure containing valves that prevent the return of the blood to the heart. The conus is another accessory chamber. It discharges into the ventral aorta or into the bulbus, an enlarged part of the base of the ventral aorta, which serves to keep the pressure on the capillaries of the gills constant. Only teleosts and a few other vertebrates have a bulbus arteriosus. There is a reduction in the conus and the number of valves in the teleosts, where only one set of valves is present.

The most notable change in the heart of fishes occurs in the lungfishes, where a circuit exists for the return of the blood from the swim bladder to the heart. The heart also has a division of the atrium, resulting in a small, partially separated left atrium for the reception of the blood from the swim bladder. In the distribution of the blood from the heart, a condition similar to that of the amphibians is set up, in that the blood from the swim bladder is directed to the body rather than to the gills. The lungfish condition approaches quite closely

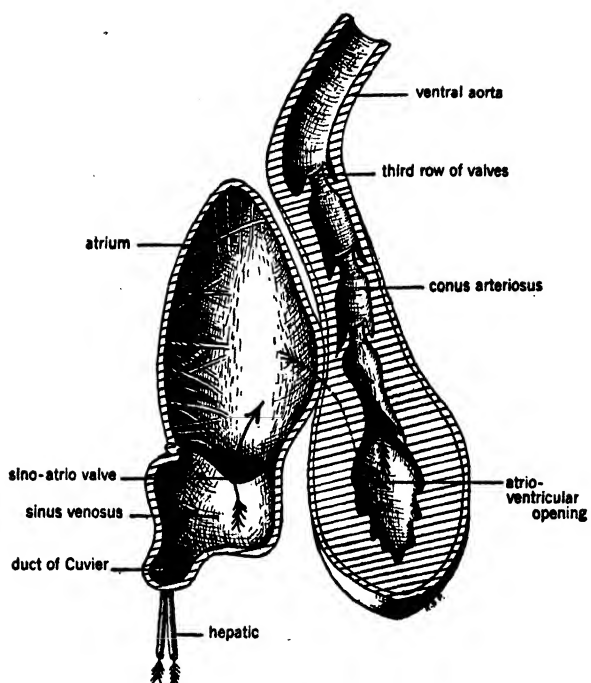
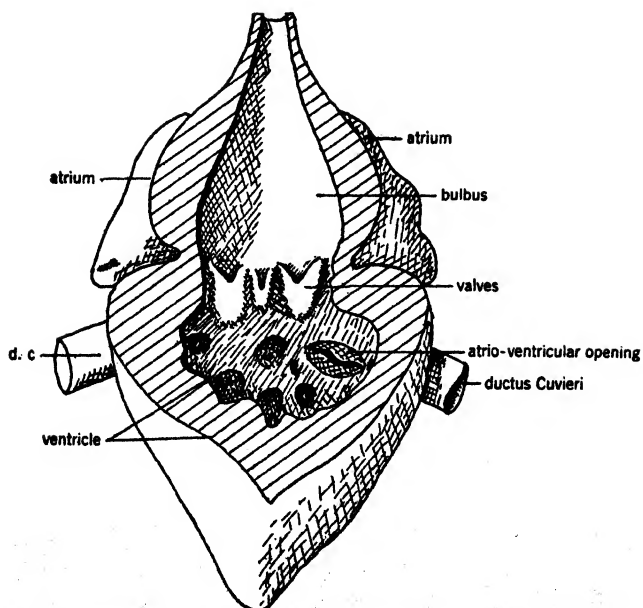


FIG. 227. Heart of a shark.

FIG. 228. Heart of a salmon (*Salmo salar*). After Goodrich.

that of the urodeles, the lowest of the living tetrapods. A comparison of the hearts of urodeles and lungfishes suggests considerable relationship. As paleontological research indicates that the paired lungs of each are a heritage from some remote common ancestor, it is to be expected that such a relationship should exist in the circulatory system.

The lungfish heart is striking in at least two particulars: first, because of the fact that the blood from the swim bladder returns to the left side of the atrium; and second, because of the development of a partial septum between the two sides of the atrium. The conus has a spiral twist, and the distribution of the blood is similar to that of the urodeles in that the best blood goes to the body while the poorest returns to the swim bladder and gills. Crossopterygians probably had the same type of a heart.

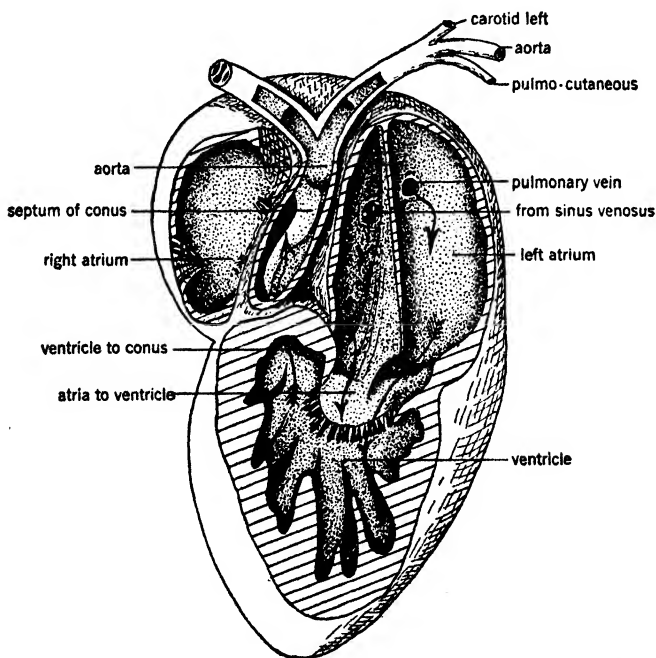


FIG. 229. Heart of frog dissected to show interior structures. After Kerr.

Heart of Amphibians

The amphibians (Figs. 229, 230) have developed three major chambers in the heart. The sinus venosus and the conus are retained. The respiratory system of the amphibians is a lung-gill-cutaneous system, and, since all three need heavy blood supply, the circulatory system may be modified. The amphibian heart continues changes that were suggested in the adaptations of the lungfishes to air breathing. With

lungs as a means of aerating the blood, and a return of this blood to the heart, the heart became three-chambered by the division of the single atrium into a right and a left half thus forming what are known as two atria. The left receives the blood from the lungs and the right the blood from the body and the cutaneous system. Even within the amphibians, there is considerable variation. The lungless salamanders, generally living in swift streams, have lost both trachea and lungs. These lungless animals must depend entirely upon the cutaneous system and the highly developed buccal-pharyngeal region, where the capillaries act as lungs. The urodeles that retain gills throughout life, as *Siren* and *Necturus*, have poorly developed lungs that are little more than sacs, but the heart has a divided atrium and there is a slight separation of the different bloods, although the lungs have little to do with aeration. The conus is simple in these urodeles, and the spiral fold is lacking, as it makes little difference into which arch the blood goes after it leaves the ventral aorta. The bulbus is present in the base of the aorta. Urodeles that lose their gills have a much better lung, for they depend on the pulmonary and cutaneous systems for aeration. Those urodeles that go to land and lose their gills develop spiral folds and valves, so that the blood entering the ventral aorta is directed into a pulmo-cutaneous stream and a systemic stream for the body.

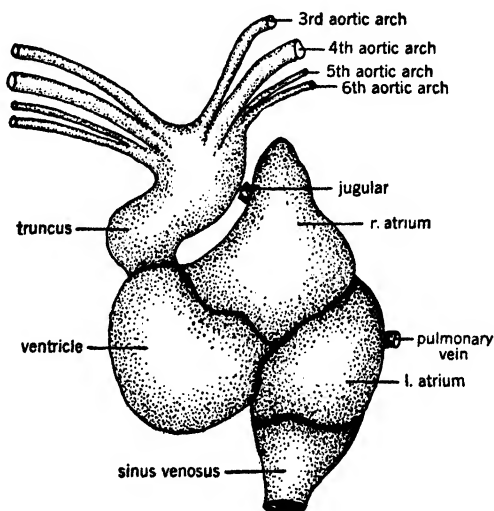


FIG. 230. The heart of *Ambystoma*.

The toads and frogs have the highest type of heart, approaching that of the reptiles, since the ventricle has numerous trabeculae, which partially separate it into two parts. Although the separation of the blood is by many trabeculae aided by a spiral valve in the conus, the delivery to proper channels is surprisingly accurate, the blood from the lungs going to the body and that of the body to the lungs. The amphibian heart is folded in an S-shape so that the atria are dorsal to the ventricle and in a more favorable position to deliver the blood into the ventricle through the atrio-ventricular valve. From the position of the right and left atria, the blood, when dropped into the ventricle, is

for the instant unmixed, the blood from the right atrium being nearest to the conus while that from the left atrium is at the posterior region of the ventricular chamber. In systole, when in turn the ventricle contracts, the venous blood enters the conus and is guided by the spiral flap into easy channels, through the sixth arterial arches to the lungs. With these filled, the remaining blood is forced through the other arches to supply the body. The cutaneous system acts as an accessory, to enrich the blood supply. The blood of amphibians is never pure, except in the pulmonary veins, but there is a fair separation of the venous and arterial bloods, primarily through mechanical specializations of the heart rather than because of separate blood channels.

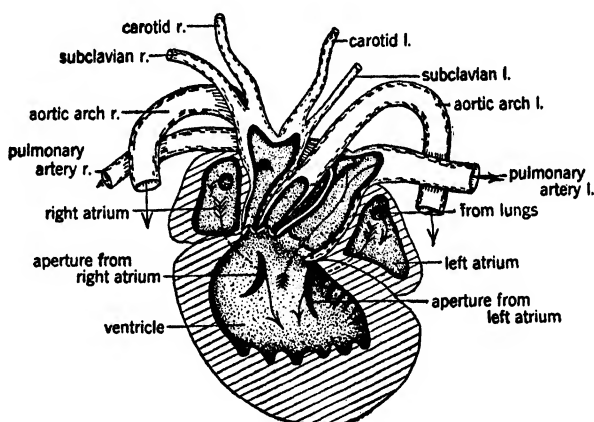


FIG. 231. Heart of turtle (*Chelydra*), dissected to show internal structure.

Heart of Reptiles

The reptilian heart (Figs. 231, 232, 233) varies from a type not much above that of the amphibians to a type approaching that of the mammals. The heart of the lower reptiles has an interatrial septum dividing the atrium into right and left halves as in the amphibians. The ventricle has advanced over that of the amphibians by developing a septum which partially divides the ventricle into right and left halves. The aorta and the conus are split to the base, so that the pulmonary artery leaves the heart as a separate vessel. The right and left arches of the aorta also are separated at the base of the conus, so that three trunk arteries leave the heart—a pulmonary and a right and left systemic (aorta) artery—each retaining valves at its base which are remnants of the conus arteriosus. The sinus venosus is still present but is closely joined to the right atrium.

The highest development of the reptilian heart occurs in the Crocodilia where it approaches the conditions of the mammalian heart. The

crocodilian heart has the ventricle completely divided by a septum into right and left halves. However, the complete separation of the

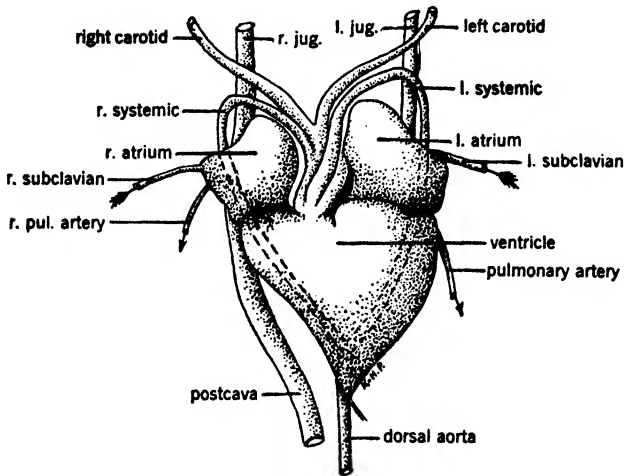


FIG. 232. Ventral view of the heart of *Sceloporus*.

aerated from the non-aerated blood is not achieved. The left aorta leaves the right side and carries non-aerated blood but the right aorta

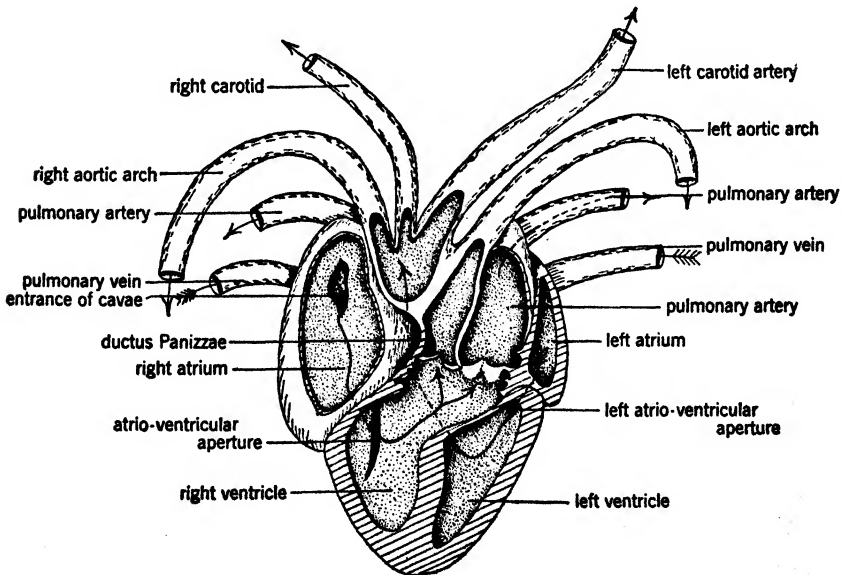


FIG. 233. Heart of alligator, dissected to show internal structure.

which sends vessels to the head, leaves the left side and carries aerated blood. Both aortae join to form the dorsal aorta which conse-

quently has some mixed blood. There is a small opening between the aortae at their base, the ductus Panizzae (Fig. 233), that permits some leakage, but it is rather small. It is not unreasonable to suppose that some of the extinct reptiles, such as the dinosaurs and pterodactyls, also had a four-chambered heart.

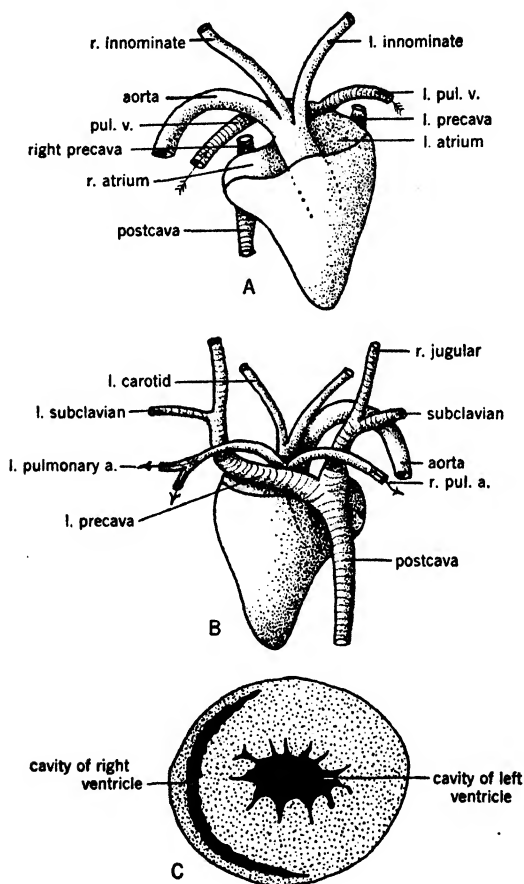


FIG. 234. Heart of chicken. A, ventral; B, dorsal; C, cross-section of ventricles.

Heart of Birds

The bird heart (Fig. 234) is divided into four perfectly separated chambers, and there is no intermingling of the blood at any point. The bird, with its very active life, might fare poorly with any mixture of arterial and venous blood. The sinus venosus is practically obliterated as it has been incorporated into the right atrium. The right ventricle remains a thin-walled chamber that partly encircles the left and pumps blood only into the pulmonary artery. The left ventricle

is heavily walled, and it forces the arterial blood to all parts of the body. The atrio-ventricular valve is completely divided by a septum formed by the fusion of the endocardial cushions which function as dorsal and ventral valves in the Amphibia. Though highly specialized, it is still a modified reptilian heart retaining only the right aortic trunk which leaves the left ventricle. The left aortic trunk has disappeared.

Heart of Mammals

See (Figs. 235, 236, 237, 238). Mammals as well as birds achieved a four-chambered heart, but coming from different lines of reptilian ancestry, they did it in different ways. The heart of the mammal is

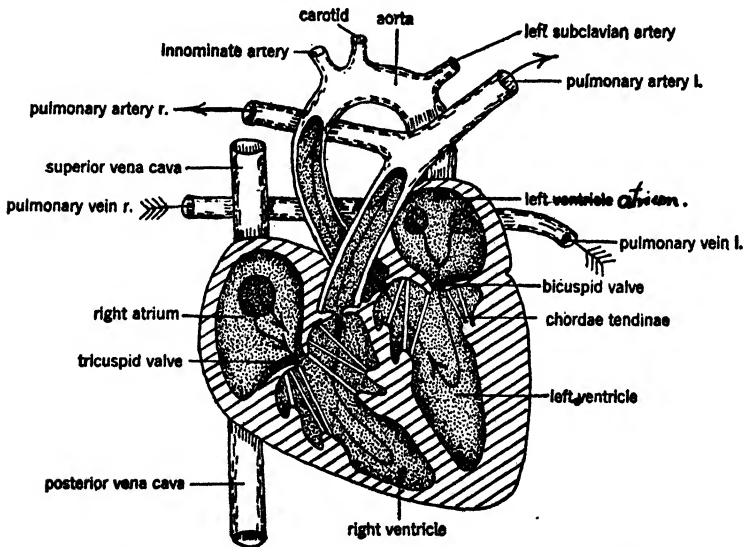


FIG. 235. Diagram of mammalian heart. Modified from Pearse and McLeod.

equal to that of the bird in efficiency, and is the same double pump, with a complete separation of the blood at all times. The sinus venosus has entirely disappeared as it has been incorporated into the right ventricle. The conus, which became split in reptiles, remains only as semilunar valves in the base of the aorta and pulmonary arteries. The blood, brought in from the head region through the superior cavæ and from the posterior region through the posterior cava, enters the light-walled right atrium, where it is held until it is sent to the right ventricle. The atria are quite distensible and are able to handle an extraordinary rush of blood. From the right atrium, the blood is sent through the tricuspid valve to the more muscular right ventricle, which sends it to the lungs for the exchange of gases. This is a light task,

the walls of the ventricle are comparatively thin in contrast to the heavy left ventricle. Semilunar valves, remains of the old conus, prevent the backflow of the blood from the pulmonary arteries. The left atrium, which receives blood from the lungs, is also rather light-walled and capable of distension. The blood from the lungs may come through one or more openings. Forced from the left atrium, the blood goes through the bicuspid valve (mitral) to the left ventricle. The left

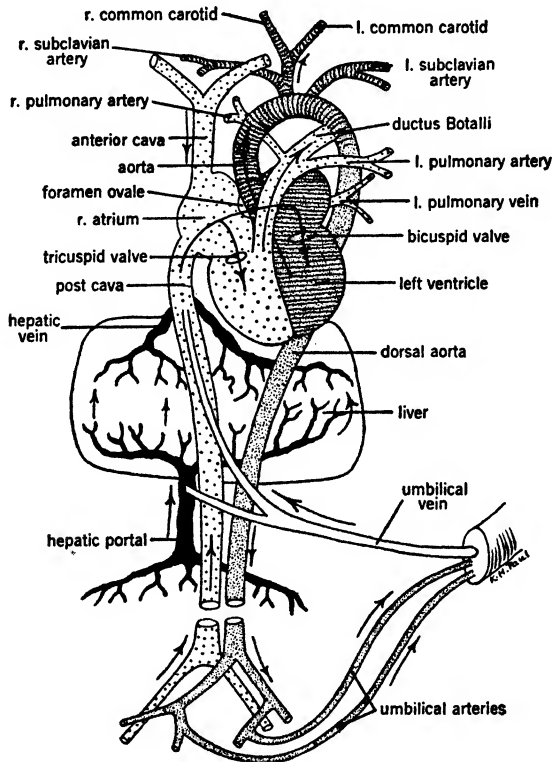


FIG. 236. Embryonic circulation of a mammal. After Weber.

ventricle is heavy-walled and forces the blood through the aorta to all parts of the body. Only a single aortic trunk is present, and this seems to be derived from the reptilian aorta before the reptiles split the aorta. The bicuspid valves are very heavy, and the chordae tendinae and papillary muscles are sufficiently strong to prevent the forcing back of the cusps (Fig. 237). The outlet through the aorta is protected by semilunar valves relics of the old conus, which prevent any backflow from the aorta during diastole.

In embryos of mammals (Fig. 236), a foramen ovale forms a connection between the atria, and some of the blood may pass through this

channel and thus avoid going to the lungs. Investigations seem to show, however, that this valve is too small to permit much blood to go through. A short time after birth, or at the end of a few days, this foramen becomes more or less obliterated by a fold of muscle from the septum. In adult animals, it is often large enough to admit a small probe, but it is protected by the septal valve, and probably no blood can go through. Some human cases have been observed in which this foramen was large (10 millimeters) and remained open throughout life.

The valves of the mammalian heart are simple but very efficient, consisting of cusps of tissue anchored by heavy chordae tendinae, which

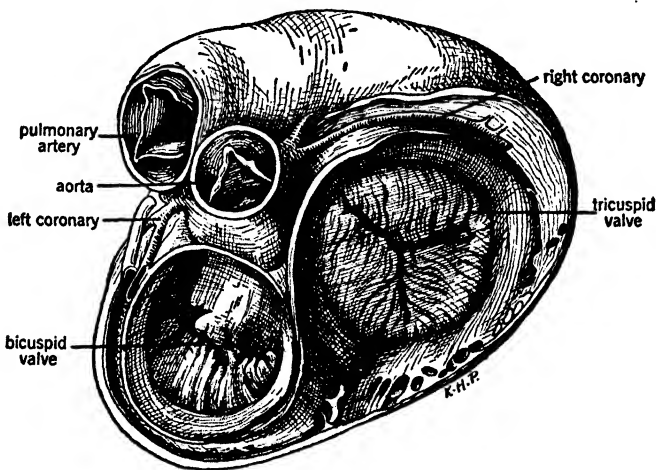


FIG. 237. Cross-section of the human heart, between the atria and the ventricles, to show the atrio-ventricular valves. After Toldt, Hochstetter.

are attached to the walls of the ventricles by papillary muscles, thus preventing any possibility of their being pushed through *in systole*, when the blood is forced out of the ventricles. The heart beat consists of, first, the contraction of the atria, and second, the contraction of the ventricles; and the contraction is paired, first the two atria followed immediately by the two ventricles in the four-chambered heart. The heart beat is initiated by the atrio-ventricular nodes and distributed by the atrio-ventricular bundle (Fig. 238) or the bundle of His. This neuromuscular bundle extends down the septum between the atria and ventricles and spreads over the heart, sending branches to the different regions. This bundle synchronizes the heart beat. Vessels leaving the heart are provided with semilunar valves to prevent backflow of blood. Both the aorta and pulmonary arteries have these protecting valves. Incoming vessels of the right atrium are also provided with valves, con-

sisting of folds of the endocardium that are somewhat rudimentary. The Eustachian valve is a slight endocardial fold along the posterior border of the inferior vena cava. The valve of Thebesius protects the entrance of the coronary sinus as it enters the atrium. The innervation of the heart is through the vagus nerve (X), which acts as a depressor, and the autonomic, which acts as an accelerator. Although supplied with nerves, the heart seems to be somewhat independent of them, for, even if all the nerves are cut away, the heart tissue will continue to beat for a

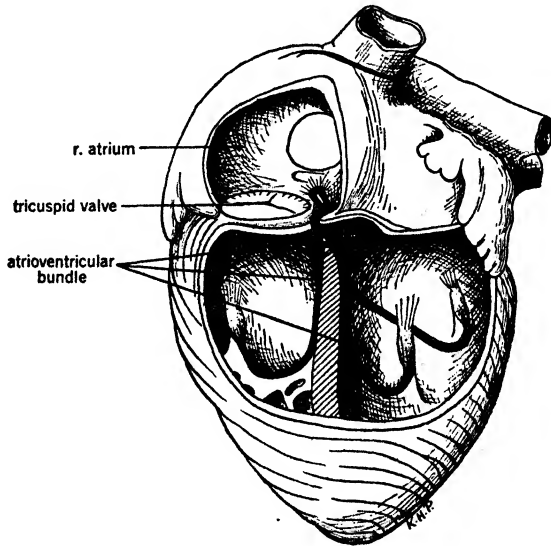


FIG. 238. Mammalian heart to show atrio-ventricular bundle or bundle of His.
After Bolk, Göppert, Kallius, Lubosch.

long time, even for years, under the proper conditions. The heart is enclosed in a pericardial sac, filled with a serous fluid in which the heart beats with a minimum of friction. The pericardial sac is held in place by the large vessel entering at the anterior end and the attachment to the diaphragm at the posterior end.

Coronary Circulation

The heart does not receive oxygen and food from the blood it pumps but depends on a small system of arteries and veins to bring blood to its tissues and carry away the waste. In fishes, the blood is distributed to the heart through the hypobranchial arteries, which receive aerated blood from the branchial arteries of the third gill and sometimes other gills. These arteries pass posteriorly and send blood into the coronary arteries and to the pericardial wall.

In mammals, the blood supply of the heart is furnished by the coronary arteries arising from the aorta just after it leaves the heart. In some mammals the coronary veins receive the blood from the capillaries of the heart and return it to the right atrium through the coronary sinus. In mammals possessing two precavas, the coronary veins empty into the base of each precava. In those that retain only the right precava, the base of the left is retained as a vestige and forms the coronary sinus (Fig. 239) which crosses the dorsal wall of the heart and empties into the right atrium at the base of the precava. The lymphatic system is well distributed over the entire heart.

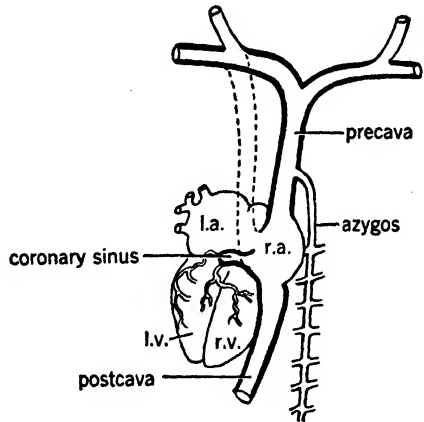


FIG. 239. Dorsal view showing condition common in many mammals retaining only the right precava. Dotted lines show lost left precava represented only by coronary sinus at base.

Arterial System

Primitively, the arterial system was segmental, but in higher vertebrates this has been modified so that little remains to show the original structural pattern. Remnants still appear as small vessels, but they are so insignificant that they are hardly recognized as such. The vertebrates tend to establish large trunk lines to regions where the supply is needed, and thus eliminate the need of small vessels. The arterial system changes much less than the venous, and there is a general similarity in the arterial branches in all classes of vertebrates. The most striking changes occur in the aortic arches. (See Fig. 240.)

The vertebrate arterial system may be divided into three regions, the head and neck arteries, the aortic arches, and the arteries of the lungs and trunk region. In the primitive arterial plan the blood leaves the heart through the ventral aorta and is distributed to the gills through a series of afferent branchial arteries. From the gills the blood is collected by a series of efferent branchial arteries which empty into the dorsal aorta. The dorsal aorta was probably paired at one time, at least in the branchial region, but is single in all living vertebrates. Each pair of afferent and efferent arteries constitute an aortic arch, and the primitive plan apparently was based on six pairs of arches. The major changes of the arterial systems of the different vertebrates are largely concerned with modifications of the aortic arches due to the shift from gill to lung respiration. These modifications will be

discussed later under the descriptions of the aortic arches of the various vertebrates.

Head Arteries

The head and neck always have special vessels, and this set of vessels becomes more prominent as the neck and head become more distinct from the body. The head always has its own vessels, the carotids for

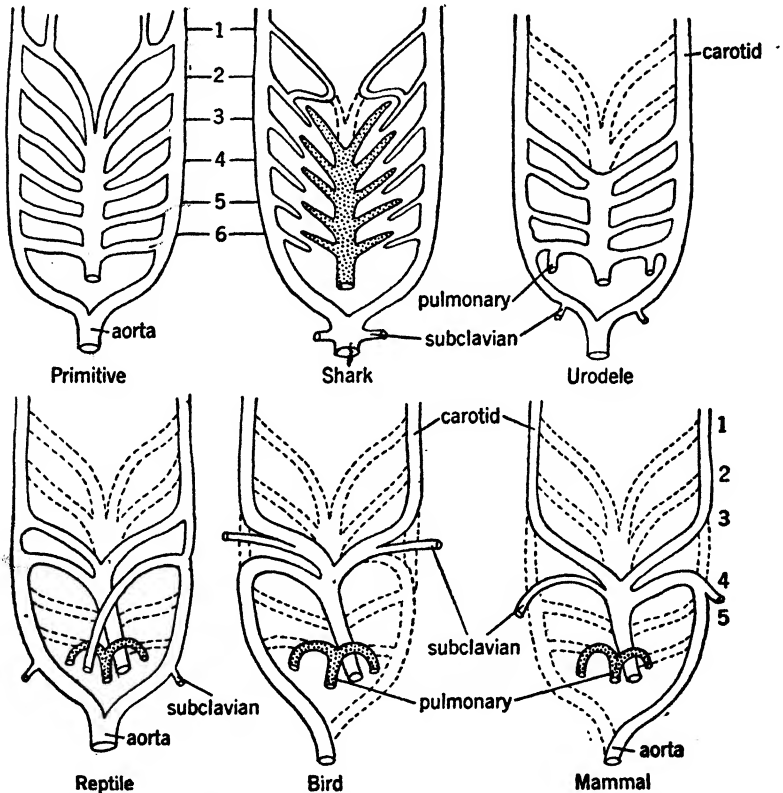


FIG. 240. Diagram of aortic arches in the vertebrate classes.

a supply and the jugular for a return. The so-called carotid system of the shark is rather small, since the supplying aortic arches are so close. As part of these vessels are remnants of the first aortic arches, it is difficult to make exact homologies with similar vessels in tetrapods. Remnants of the paired aortae (Fig. 241), extending anteriorly to the first gill, can be seen in the tiny so-called vertebral arteries of the shark. The spiracle of the shark, representing the first gill cleft, is served by the afferent spiracular artery, formerly called hyoidean, which represents the first afferent branchial artery. The blood leaves

the spiracle by the efferent spiracular artery (ventral carotid), which represents the remains of the first efferent branchial but now sends blood to the head. The second efferent branchial artery has been modified and is represented by the efferent hyoidean artery (common carotid); it now carries blood forward to the head from the pretrematics of the second gill cleft.

Because of the close proximity of the aortic arches, other vessels creep into the head region, but these are eliminated as the neck becomes more extended. The brain receives a part of its arterial sup-

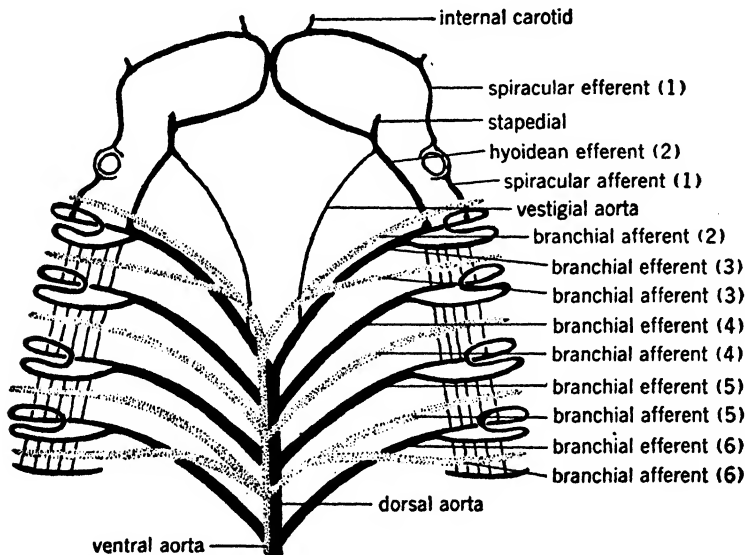


FIG. 241. Diagram showing aortic arches of dogfish shark (*Squalus acanthias*).

ply from an artery that comes through the foramen magnum. The internal carotid of the elasmobranchs enters the brain case through a foramen just posterior to the optic chiasma and joins with the vessel that comes through the foramen magnum, thus making an anastomosis with the blood system that lies ventral to the brain, the circle of Willis and the meningeal branches. The stapedial artery (external carotid) leaves the first efferent artery and supplies the head region outside of the brain case, including all the superficial regions. It is rather difficult to determine the relations of these vessels to the carotids of the tetrapods, and we may assume that numerous changes took place before the tetrapod series emerged.

The carotids are somewhat puzzling in the lower urodeles (Fig. 243), since they have retained a part of the gill system; but in anurans the picture becomes more clear cut, with paired common carotids that bifurcate to form internal and external branches. The carotid stem now

comes off the fourth aortic arch and is formed from parts of the lost second and third arches. The subclavians originate well anterior on aortic arch four, but they are separated from the carotids. Among tetrapods, there is often a close association between the carotid stem and the subclavians (Fig. 250).

There is a wide range of variation in the reptiles, in which the subclavians may be completely separated from the carotid stem. *Lacerta* has a common carotid formed from the third aortic arch, and there are two symmetrical stems from which the internal and external carotids take origin. The subclavians originate far down on the stem of the fourth arch, this having no relations at all with the carotids. *Varanus* has a single carotid stem from which the common carotids originate; *Emys* has the subclavians and carotids of each side coming off together. Some peculiar conditions are found in the limbless reptiles, where the subclavians are entirely absent. *Sphenodon* has a rather primitive set of aortic arches; the third, the fourth, and the sixth are complete, and all retain connections with the aorta.

In birds (Fig. 249), the paired carotids originate from large innomines, each of which gives off a subclavian and common carotid for its side. Since only the right fourth aortic arch is present, the type is somewhat fixed. The carotids really appear to come off from the subclavians. The common carotids extend to the head region before dividing into internal and external branches.

The carotids come from the left fourth aortic arch in all mammals and are usually somewhat related to the subclavians. There is a great deal of variation among the mammals themselves in the relations of these two sets of arteries. The external carotids extend along the side of the head, staying rather close to the lateral side of the skull, and in the alisphenoid region may be encased in a sheet of bone which forms an alar or alisphenoid canal. The internal carotid is given off at the posterior part of the skull and enters the jugular foramen to supply the brain and its coverings (Fig. 252).

Trunk Arteries

The aorta posterior to the heart extends posteriorly to the tail region, if a tail is present, or forms a vestigial caudal if the tail is missing. There is a great similarity in the vessels given off by the aorta after it starts down the body. Along its length, there are always small vessels that have the character of segmentals, but they are small and insignificant. Small segmental arteries that supply the back muscles and the spinal cord enter the body wall along the greater part of the length of the aorta. The usual sequence of the major unpaired arteries supplying the viscera appear in the shark. Inside the body cavity, the

coeliac axis is first, supplying the anterior part of the digestive tract and the liver. An anterior mesenteric artery supplies part of the digestive tract: a third, the lienogastric, supplies the spleen and a part of the digestive system. These last two arteries constitute what is known as the superior mesenteric artery in some vertebrates. The last visceral artery in the shark is the posterior mesenteric which passes to the posterior part of the digestive tract. The mesonephroi are supplied by small segmentals along their length.

Above the cyclostomes two major sets of paired arteries for the appendages occur in all vertebrates possessing paired appendages. The first pair are the subclavians which pass out into the fore limbs or pectoral fins. After giving off branches within the trunk, these usually are known as brachial arteries within the appendages. They leave the aorta near the base of the aortic arches in the lower vertebrates but move anterior to the functional arches as the neck lengthens and the heart is pushed backward in the higher vertebrates. Posteriorly the paired iliacs supply the pelvic fins or hind limbs. The iliacs usually become known as the femoral arteries after entering the appendages. In all vertebrates, the plan of the major arteries is similar. The gonads have their own arteries, and in mammals the renal arteries are reduced to one for each kidney. Elongated animals show the coeliac and other unpaired visceral arteries merely as a series supplying the length of the digestive tube. *Siren*, *Cryptobranchus*, and *Necturus* show varying degrees of this type of distribution to the alimentary canal. A frog, however, has a well-defined coeliac axis. Numerous changes in the arteries occur in connection with the development of limbs, and the arteries keep pace with the limb development. In mammals, there is much similarity in these trunks, since they supply structures of a like type and position. The trunk arteries come off both as single or paired branches, since paired organs usually have paired vessels. The coeliac axis, anterior and posterior mesenterics, are single trunks; while those that supply the kidneys, ovaries, testes, lumbar and leg regions are paired. The abdominal aorta of the dog has the following branches: series of intercostals; coeliac axis; superior mesenteric; phrenico-abdominal; inferior mesenteric; renals; spermatics; iliacs; and internal iliacs. Those going to paired organs have paired trunks. In man a similar line of arteries supplies the body, and, with minor variations, the same system is to be found generally in the mammal group.

The Aortic Arches

The aortic arches consist of pairs of afferent and efferent branchial arteries that carry blood to and from the gills of the lower vertebrates. They persist partly in the higher vertebrates although performing

other functions. These vessels connect the ventral aorta with the dorsal aorta, through which the arterial blood is directed to the different parts of the body. The arterial arches lie on the outside of the gill bars or visceral arches. Because of their persistence in the developmental stages of vertebrates, they are of great interest to embryologists and

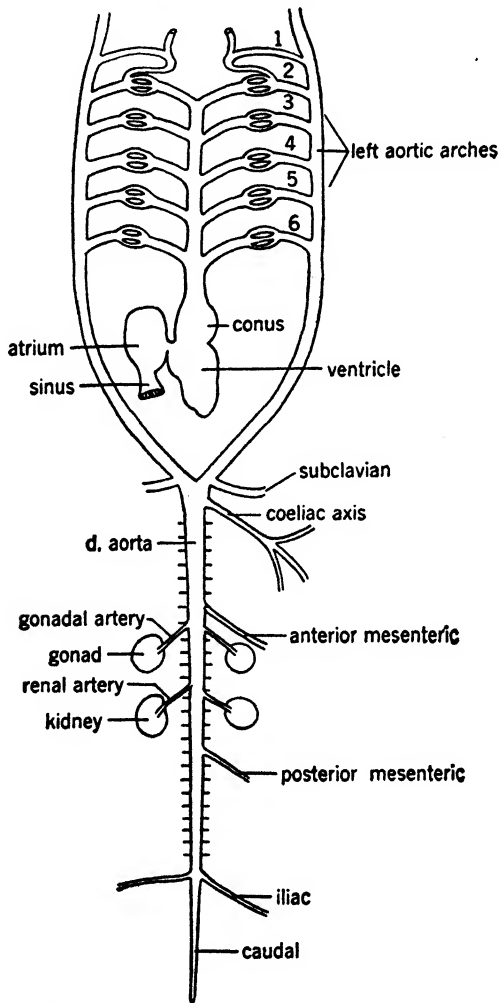


FIG. 242. Diagram of arterial circulation of a shark.

anatomists (Fig. 240). The primitive plan of the arches consists of six or more pairs of arches, each passing through a gill; but in modern fishes only four or five may function. In the dogfish shark (*Squalus*), the second, third, fourth, fifth, and sixth send blood to the aorta. The codfish (*Gadus*) has four functional arches; the primitive elasmobranch

(*Heptanchus*) has seven. The spiracle of the sharks is their first gill slit, and it is non-functional as a gill, although remnants of the first gill still remain. With minor modifications, living fishes retain this

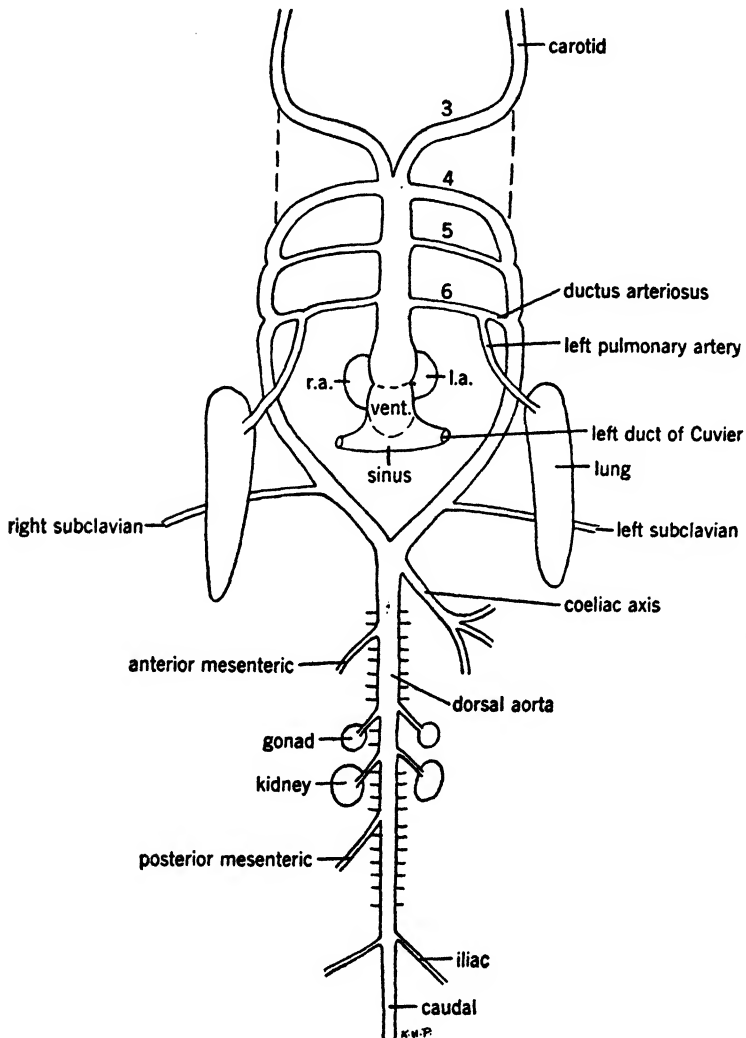


FIG. 243. Diagram of the arterial system of an amphibian (Urodele). Ventral aspect.

plan of the arches, although lungfishes alter it by sending the blood of the sixth arches back to the heart after its contact with the swim bladder. The arches are usually numbered from anterior to posterior so that the most posterior pair of arches is the sixth.

Arches of Amphibians

The arches of the amphibians are changed by new tetrapod features (Figs. 243, 244), principally the introduction of lungs as the main respiratory structures, and the diminishing importance of the gills.

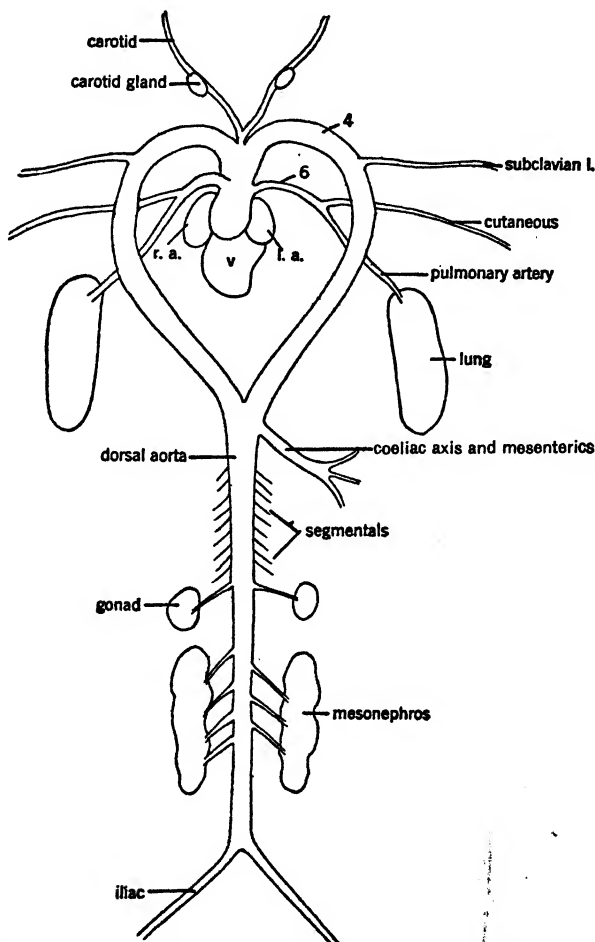


FIG. 244. Diagram of the arterial system of an amphibian (frog).

The sixth pair of arches diverts all or part of its blood to the lungs by sending off new vessels, the pulmonary arteries. Two different patterns exist in the amphibians: first, the arrangement in those that remain in the water and retain the gills in adult life; and second, the arrangement of the arches of those that lose the gills in adult life, as in the anurans and some urodeles.

Urodeles, retaining the gills permanently, make some partial shifts in the aortic system: (1) each sixth aortic arch sends a pulmonary

artery to the lung but retains its connection with the dorsal aorta as the ductus arteriosus (ductus Botalli); (2) the second and third arches, losing their connections with the gills as the gills disappear, and remain as part of the carotids passing to the head. In *Necturus*, the fourth, fifth, and part of the sixth arches transmit blood to the aorta.

The anuran (Fig. 244) continues changes started in the arches of the aquatic urodeles. The primitive arch system becomes modified as follows: (1) a further reduction or loss of the ductus arteriosus, connecting each sixth aortic arch, after giving off the pulmonary artery, with the dorsal aorta; (2) loss of the fifth aortic arches. The characteristic tetrapod condition is now established in which the sixth pair

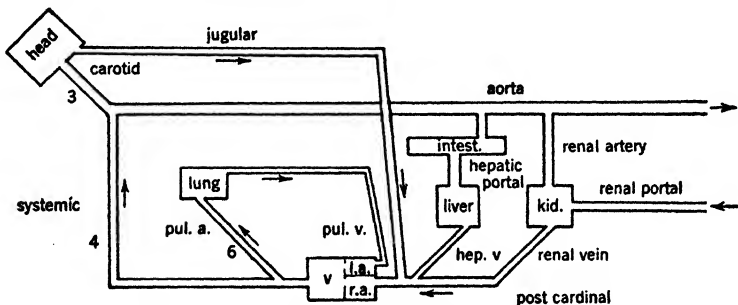


FIG. 245. Diagram of circulation in a frog.

of arches supplies the lungs only and forms the bases of the pulmonary arteries, the fourth pair of arches becomes the systemic, and the third, as well as possible vestiges of the second and first arches, become parts of the carotid system. In anurans only the fourth or systemic arches transmit blood to the aorta.

Arches of Reptiles

With the gills entirely gone, the arches of the higher reptiles form the pattern from which the arches of birds and mammals are derived. The gill system is entirely suppressed. The elongated neck region and the posterior shifting of the heart from the pharyngeal region have had a decided effect on the proportions of the arches. The following conditions have become established in the higher reptiles: (1) more complete separation of the ventral aorta into two groups of vessels as they leave the heart; (2) loss of the fifth arch; (3) reduction or loss of the ductus arteriosus, connecting parts of the sixth arch with the aorta.

Some reptiles have not advanced so far and retain primitive conditions of the aortic arches which are probably inherited from their

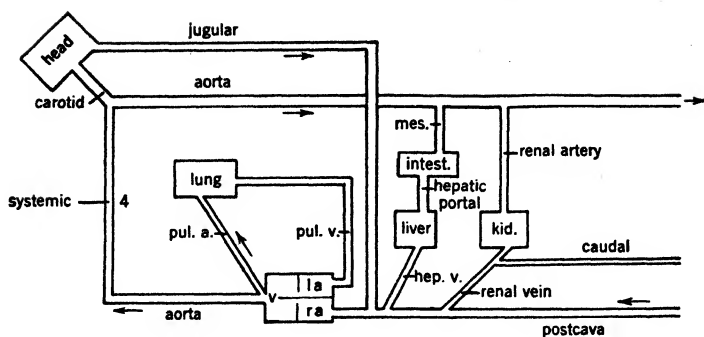


FIG. 246. Diagram of the circulation of a lizard.

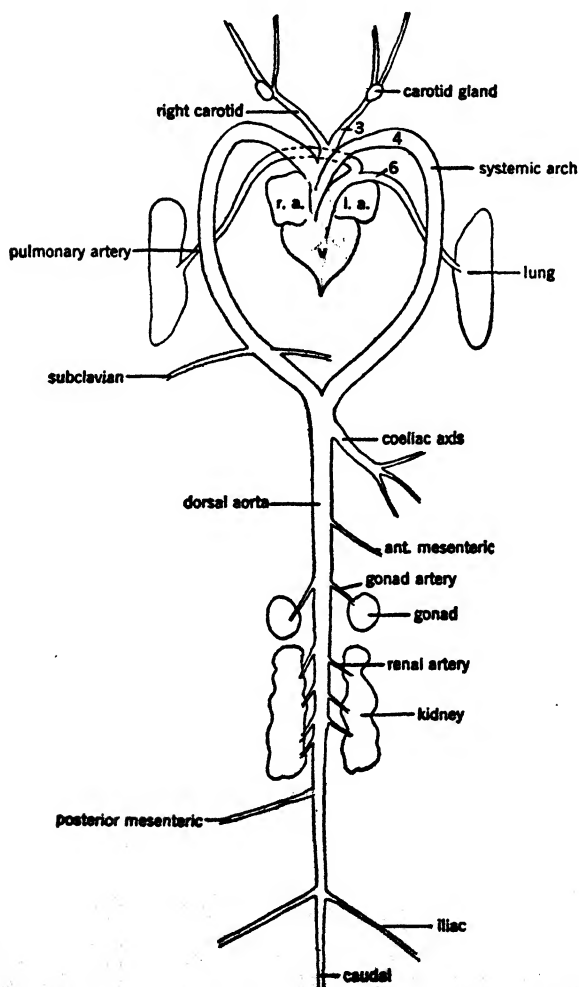


FIG. 247. Diagram of the arterial system of a reptile (lizard).

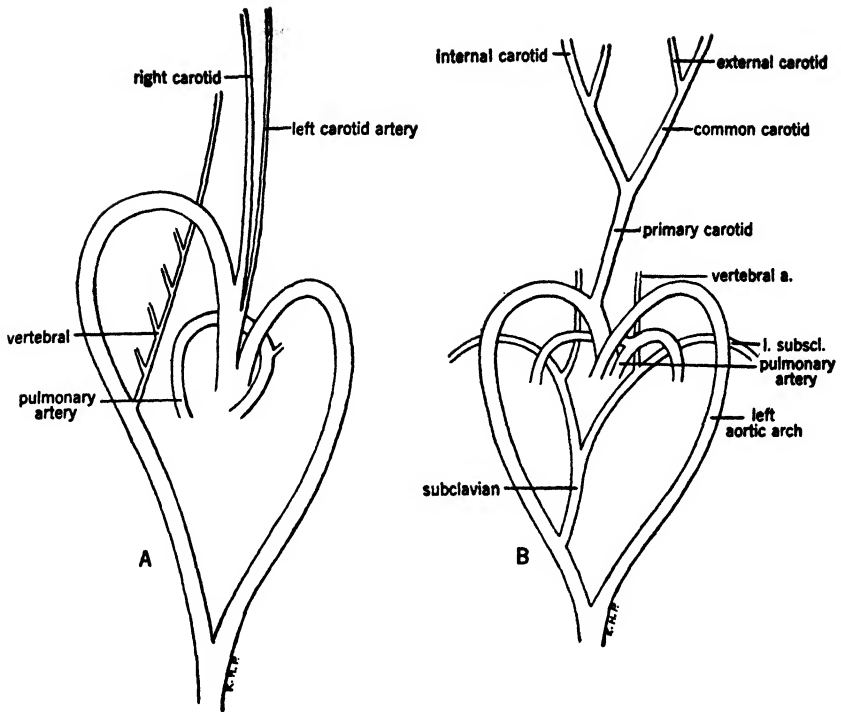


FIG. 248. Aortic arches. *A*, Boa; *B*, *Varanus*, a lizard. After Hafferl.

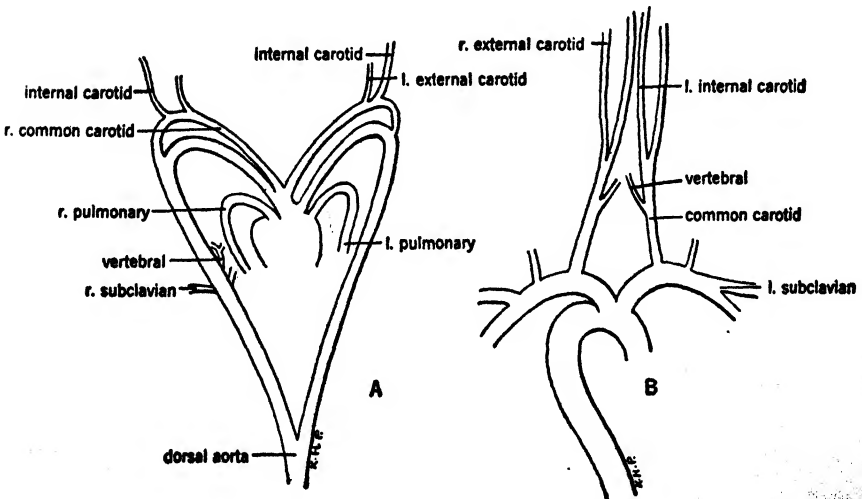


FIG. 249. Aortic arches. *A*, lizard (*Lacerta*); *B*, bird (goose). After Hafferl.

early amphibian ancestors. *Sphenodon* retains more primitive conditions than that of any other living reptile. The third pair of arches is complete and connects with the dorsal aorta, giving rise to the carotids. The fourth pair of arches is complete, except that the left arises separately from the heart. The fifth has disappeared, but the

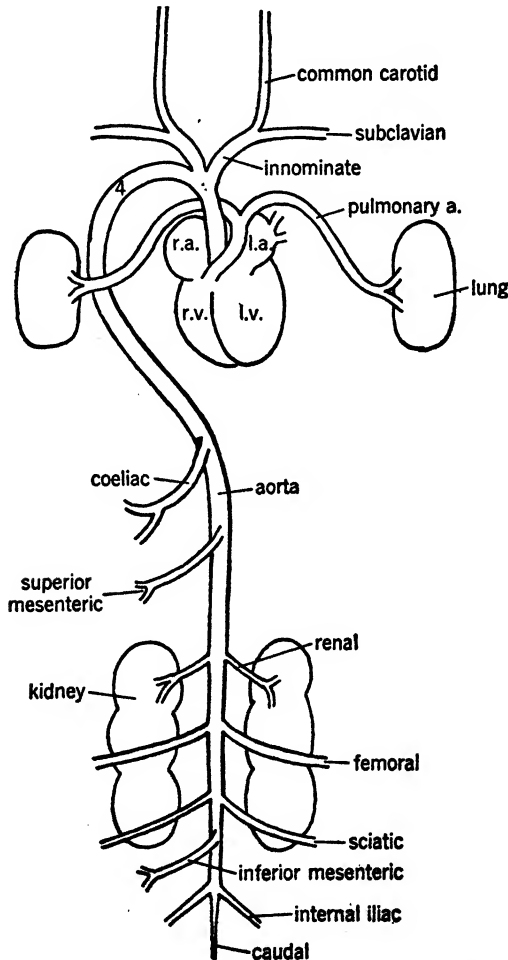


FIG. 250. Diagram of the arterial system of a bird.

sixth, after giving rise to the pulmonaries, is completed on both sides by open arterial ducts connecting with the aorta. Thus *Sphenodon* has the third, fourth, and sixth arches present and all contributing to the aorta.

In other reptiles the bases of the carotid represent remains of the third arches, which may or may not have connections with the dorsal

aorta. The fourth pair forms the main aortic arches and contributes most if not all of the blood to the aorta. The fifth arches are absent; the sixth are represented partly by the base of the pulmonaries and no

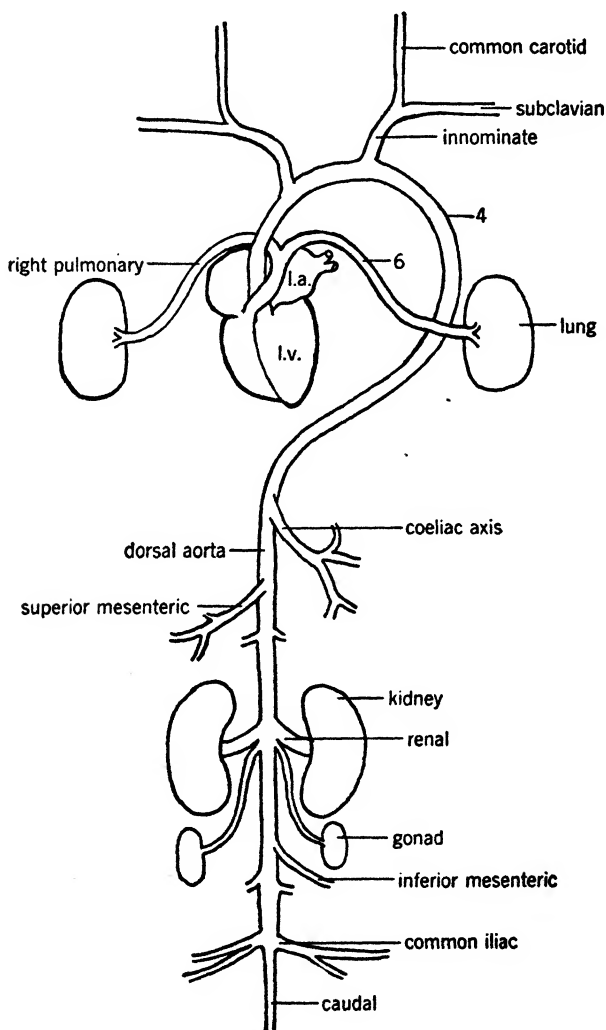


Fig. 251. Diagram of the arterial system of a mammal (ventral aspect).

longer contribute blood to the aorta in the adult, as the arterial duct is closed and vestigial.

The aorta no longer shows a distinct separation into a ventral aorta in the more advanced reptiles. In some reptiles such as *Sphenodon* the subclavian still leaves the base of the dorsal aorta, where the arches

join, but in others, where the heart is moving posteriorly, the subclavian is shifting anteriorly on the fourth arch.

Arches of Birds and Mammals

Both birds and mammals retain but a single systemic arch, the right in birds and the left in mammals. This represents the fourth aortic arch. In mammals only the left half of the fourth arch, and in birds only the right half of the fourth arch, transmits blood to the aorta. The vessels leading from the heart are completely divided, so that there is no intermixture of blood at any place in the system. As all the intermediate links are gone, and no remnant of the connection

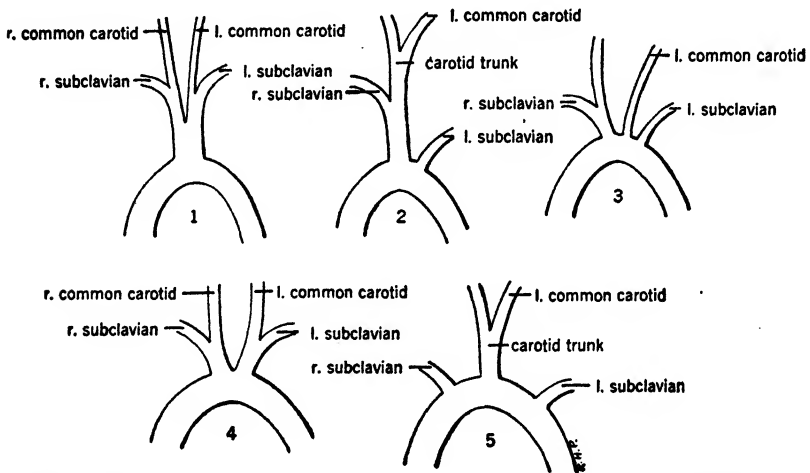


FIG. 252. Various arrangements of anterior arteries leaving the mammalian aorta. 1, *Perissodactyla*, *Artiodactyla*; 2, *Marsupialia*, *Carnivora*, *Edentata*, *Rodentia*, some primates; 3, *Monotremata*, *Homo*, *Sirenia*, some bats; 4, some *Cetacea*, *Insectivora*; 5, walrus of the *Pinnepedia*, African elephants.

between the arches is retained, all the blood must leave the right ventricle through the pulmonary artery and the left ventricle through the single aorta. The aortic arches are very important and interesting from the embryological standpoint, since those of the embryo are of the primitive fish type but gradually shift to the adult condition (Figs. 240, 250, 251). Remnants of part of the sixth aortic arch remain as the base of the pulmonary arteries. The remainder of the left sixth arch persists as the duct of Botallo, or the ductus arteriosus, carrying blood in the fetus from the pulmonary to the aorta. This connection usually closes at birth and persists as the ligament of Botallo (Fig. 236). The bases of the carotids are vestiges of the third arch. Arches one, two, and five have completely disappeared. The fifth aortic arch can be seen in the embryos of some mammals such as the cat.

Venous System

The venous system is the route by which the blood returns to the heart from different parts of the body. There have been many changes

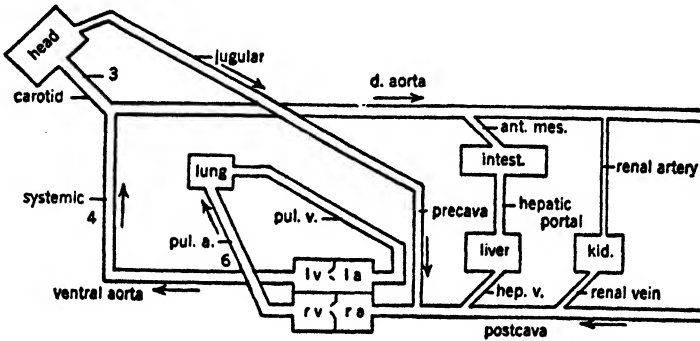


FIG. 253. Diagram of mammalian circulation.

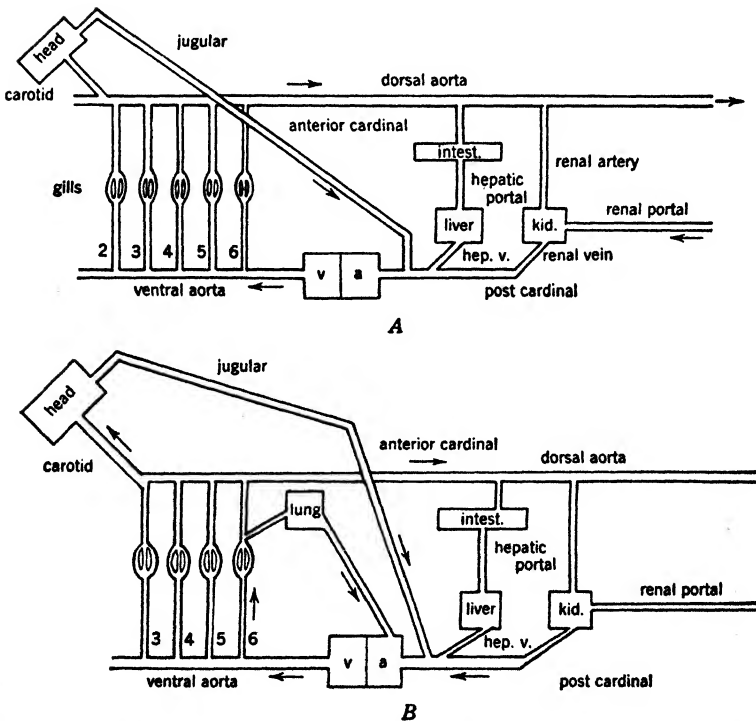


FIG. 254. A, Diagram of the circulation of a teleost. B, circulation of a lungfish.

in this system in the development of the vertebrates from fishes to mammals. Originally, it is a paired, rather symmetrical system, but with the changes that accompanied life on land and air breathing it

shifts somewhat to the right side of the body. Its history shows many parts that, rendered useless by elimination of the original structures, have been either changed and used for other purposes or dropped out altogether.

The venous system of the lower vertebrates may be divided into three distinct parts. The first part consists of the systemic veins carrying blood from all parts of the body and emptying into the sinus venosus of the heart. These include the anterior cardinals and jugulars

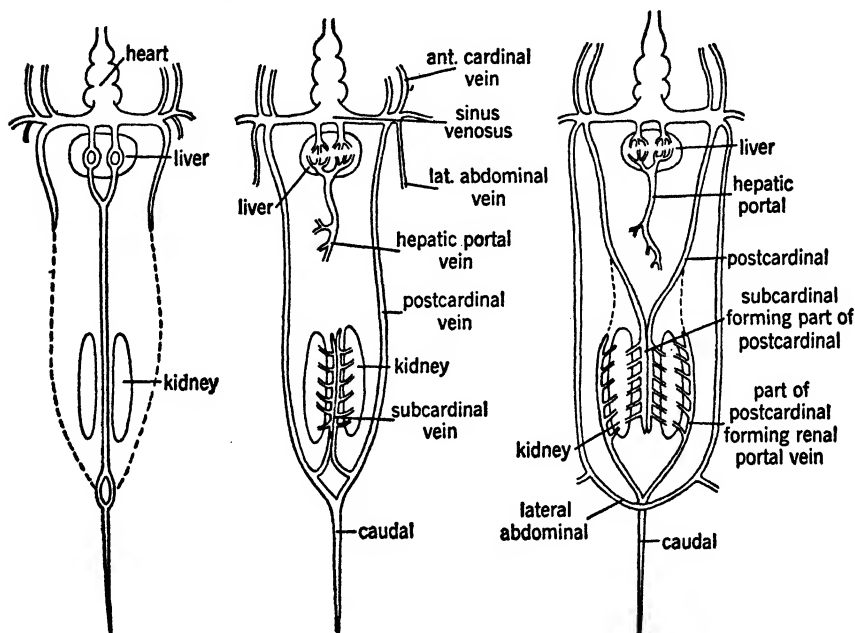


FIG. 255. Three diagrams showing stages in the development of the veins in the shark.

from the head; the subclavians from the lateral regions and anterior appendages; the postcardinals from the viscera and the hepatic veins from the liver. These veins become modified greatly in the higher vertebrates. The second part of the venous system is the hepatic portal system (Fig. 254) which carries blood from the digestive tract to the liver. This system remains very much the same in all the vertebrates. The third part is the renal portal system which carries blood from the caudal region and later from the hind legs to the kidneys. This system gradually becomes incorporated into the systemic system of the higher vertebrates and eventually by-passes the kidneys entirely. The portal systems apparently originate as portions of the systemic system, which become detached by the intervention of the liver and the kidneys.

Later, in land vertebrates, a fourth part is added to the venous system to drain the lungs. This is the pulmonary system; it consists of the veins of the lungs draining into the several pulmonary veins which empty into the left atrium of the heart.

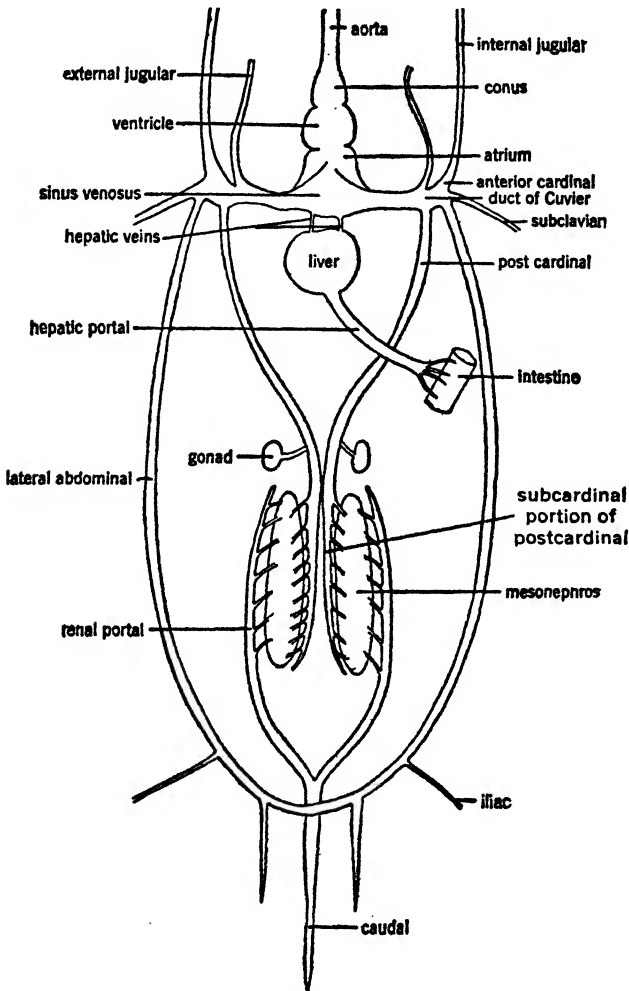


FIG. 256. Diagram of the venous system of a shark (ventral aspect).

Fishes

The venous system of the dogfish shark approaches closely the primitive basic plan for the venous system of the vertebrates. Most of the vessels are paired. Some of the larger veins expand into swollen, thin-walled structures called sinuses. The largest vessels of the venous system consist of two pairs of cardinal veins (Fig. 255), the anterior

and posterior, which are laid down early in embryonic life. Blood from the head returns to the heart through the anterior pair, and blood from the posterior parts of the body returns through the posterior pair. These empty into the ducts of Cuvier (Figs. 224, 256), or common cardinal sinuses, which are lateral extensions of the sinus venosus. The blood from the lateral walls and the pelvic fins returns through the paired lateral abdominal veins, which join the subclavians from the pectoral fins and enter the duct of Cuvier. The lateral abdominals are absent in most teleosts. The blood from the liver drains into the sinus venosus through two large hepatic sinuses. The blood from the digestive tract is carried into the liver by the hepatic portal system, which distributes the blood into the capillaries of the liver, from which it is collected by the hepatic veins and sent to the heart by the hepatic sinuses. The hepatic system consists usually of three or four major veins collecting blood from the various parts of the intestine, stomach, and spleen, then uniting to form a hepatic portal vein emptying into the liver. Aside from minor variations, there is little change in this system in the higher vertebrates.

The blood from the caudal region is drained forward by the caudal vein, which divides into two renal portal veins emptying into each kidney. From a study of the embryological development of the cardinal system of the shark, it seems that the postcardinals arise as paired anterior extensions of the caudal vein extending forward to the common cardinal (Fig. 255). Later the postcardinals separate off at the anterior ends of the kidneys and add new parts posteriorly, the subcardinals, to drain the kidneys. This leaves the caudal vein with the two detached posterior portions of the postcardinals emptying into the kidneys as the renal portals. The shark system is almost diagrammatic in its simplicity when considered as a whole (Fig. 256).

Amphibians

The circulation of the urodeles (Fig. 257) resembles that of the fish, but a number of changes accompany the shift from water to a semi-land life. The anterior cardinals become the jugulars and, losing their sinuses, empty into the Cuvierian ducts. The postcardinals, while functioning much as in the shark, are slowly being reduced in importance by the growth of the postcava, which is to supersede them (Fig. 257). The postcardinals are beginning to reduce in size, although still retaining their original connection with the mesonephros and the posterior part of the body.

In *Necturus*, the postcardinals retain connections with the renal portals, which were originally part of the primitive postcardinals. The

lateral abdominal veins have formed a connection with the renal portals. They unite anteriorly to form a ventral abdominal vein, which empties into the hepatic portal vein instead of the common cardinal. One of the most significant changes is a new vessel, the postcava, which also appears in the lungfishes and has now established itself as the main vessel from the mesonephroi. It has formed by incorpo-

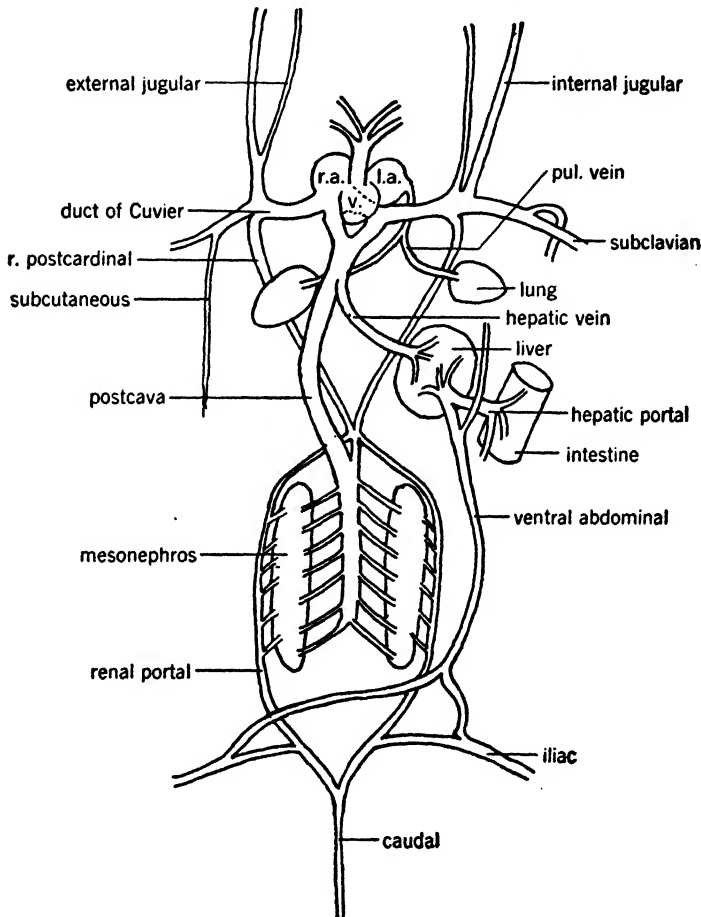


FIG. 257. Diagram of the venous circulation of an amphibian (urodele), ventral aspect.

rating the posterior part of one or both of the subcardinal portions of the postcardinals to form a new vein, which branches off at the anterior end of the kidneys and goes into the liver, joining the hepatic sinuses, through which it continues to the sinus venosus. Thus the postcava is derived posteriorly from the postcardinals, anteriorly from the hepatic sinuses, with a new portion established between. The uro-

deles retain connections between the postcardinals and the new portion of the postcava, but the postcardinals disappear in the anurans. The postcava drains blood from the kidneys and the liver and empties into the sinus venosus directly. Eventually, this vein is to return all the blood from the posterior part of the body. The lungs are small

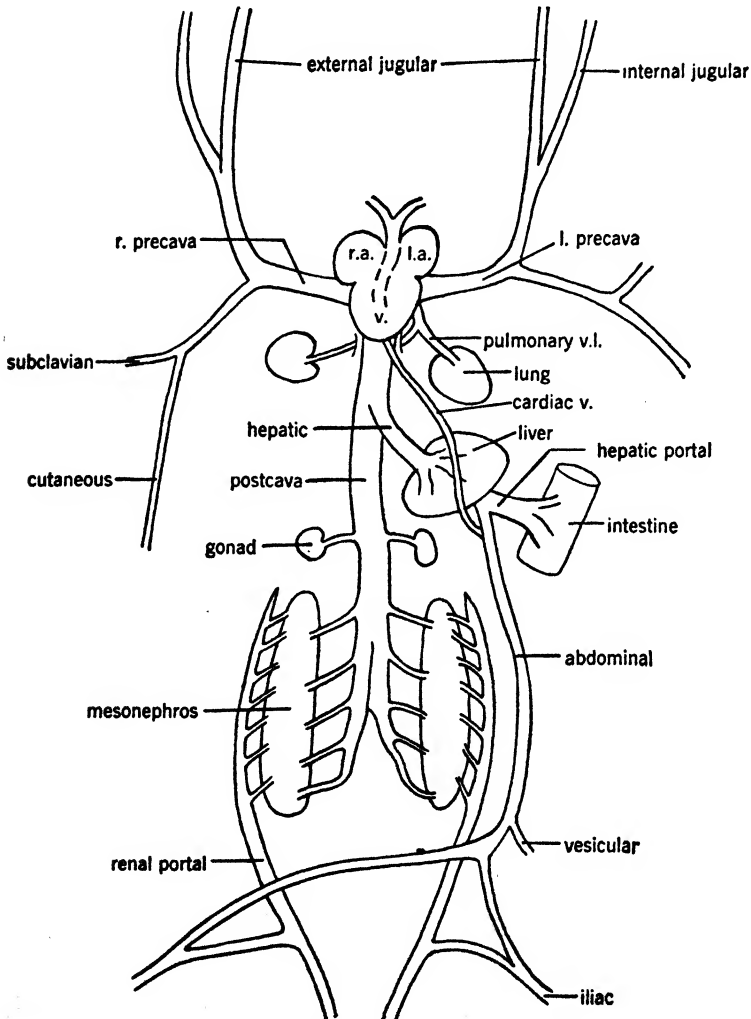


FIG. 258. Diagram of the venous system of an amphibian (frog), ventral aspect.

and not large enough to supply sufficient oxygen for the body, and two large cutaneous veins extend along the sides of the animal, somewhat similar to the lateral abdominals of the shark. The cutaneous blood comes from the subclavian artery in urodeles (pulmonary artery in

frogs) and returns through the subclavian vein. The lung circulation, also started in the lungfishes, is well established and a definite system.

The anuran venous system (Fig. 258) has lost the postcardinals entirely, which forces all the blood through the now thoroughly established postcava. The ducts of Cuvier approach the heart mesially and are known as precaval veins. Most of the remnants of the original gill system are lost in the adults. There has been considerable simplification in the anurans, and there is less indication of the older segmental vessels of the more primitive vertebrates. There is a marked increase in the arterial and venous vessels of the limbs.

Reptiles

With the further division of the heart in reptiles, there is a gradual shifting of the venous system to the right side of the body (Fig. 259). Other changes appear which are related to land life, such as the supply to the limbs. Anteriorly a pair of trunk veins, the precavae, drain into the heart. The anterior cardinals, which are represented by the internal jugulars, have fused partly with the external jugulars to form the anterior portion of the precavae. The ducts of Cuvier have formed the basal portions of the precavae. This condition continues in the birds and the mammals. The postcava has assumed the entire responsibility for returning all the blood to the heart from the posterior part of the body. The postcardinals have become minor vessels. In *Sphenodon* the anterior part of the postcardinals forms a pair of vertebral veins, draining the body wall posteriorly. These veins usually fuse and appear as a single vein in other reptiles forming part of a supracardinal system. Posteriorly remnants of the postcardinals and subcardinals are found in the renal portal and the postcaval veins.

Blood from the tail and hind legs is drained by the renal portals and connected lateral abdominals. The renal portal system is retained in the reptiles but is reduced, and less blood is passed through the kidneys. The renal portals enter the kidneys, but in some they pass on through and join the postcava. The lateral abdominals have a connection with the renal portals and carry blood from the hind legs into the hepatic portal system as in *Necturus*. In some reptiles, such as *Sphenodon*, the lateral abdominals unite ventrally to form a ventral abdominal vein. The hepatic portal system remains much the same as in the lower vertebrates, all its blood passing into the liver.

Shifts in the heart have already been mentioned. The cutaneous system of the amphibians has entirely disappeared as a special part of the respiratory system. Naturally, in a group that has so many different forms, there is a wide range of variation in the blood system associated with specializations; thus the snakes have lost one pul-

monary vein, and vessels from the non-existent limbs fail to materialize.

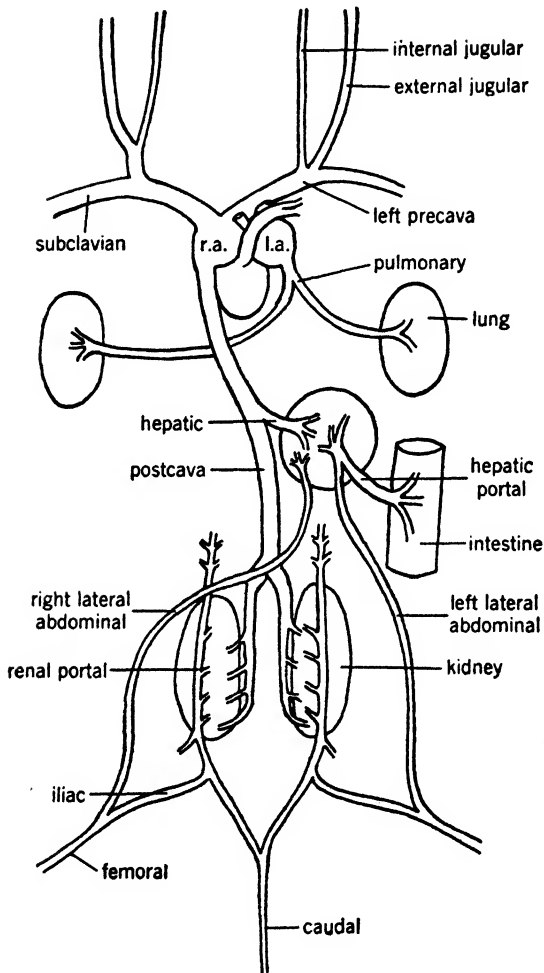


FIG. 259. Diagram of the venous system of a reptile (ventral aspect).

Birds

The venous system of birds (Fig. 260) is pushed slightly to the right and is somewhat modified from the reptilian type, although it shows its reptilian origin very plainly. The united jugulars form precavae of the same origin as in reptiles, leading to the heart, and there is often an anastomosis between right and left sides—perhaps an advantage when the neck is turned. The ducts of Cuvier are in-

cluded in the base of the precavae and are no longer separate structures. The postcava is the main vessel bringing blood from the posterior part of the body. It originates posteriorly from a union of the iliacs, which are in turn formed by the union of the femorals and renal portals. The iliac-femorals no longer have any connections with lateral abdominals. With the added importance of the limbs, especially

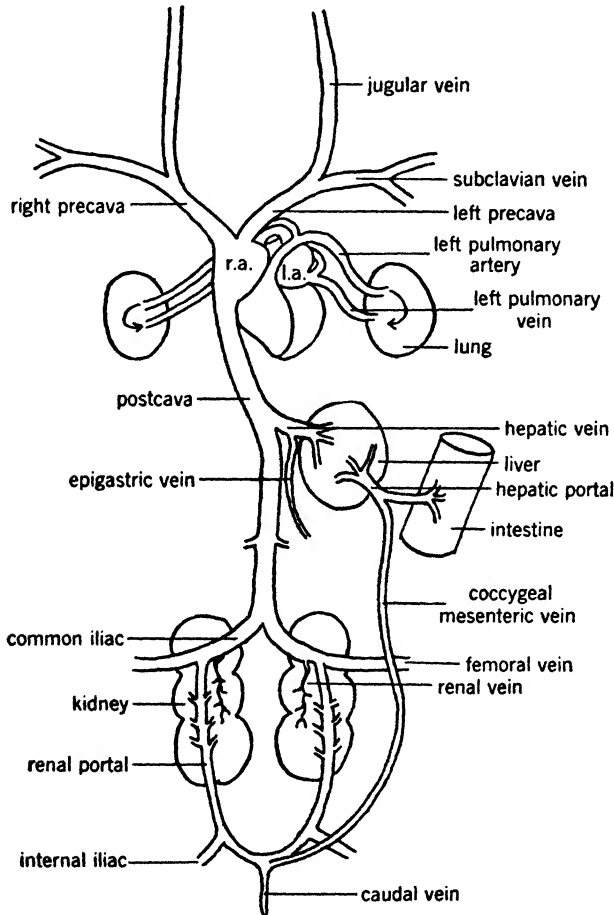


FIG. 260. Diagram of the venous system of a bird (ventral aspect).

the wings with their enormous musculature, there is a decided increase in the size of the subclavians and the iliacs of the hind legs. The subclavians have moved farther forward on the precavae. The caudal is tiny, and the renal portal has little or no relation to the kidneys, since the renal portals tunnel through the kidney tissue as they did in the reptiles and connect with the postcava through the iliacs. Some research

has questioned the lack of action by the kidneys on the blood carried by the portal system. The ventral abdominal of reptiles does not appear, but a similar vessel, the coccygeomesenteric or inferior mesenteric, drains the blood from the mesenteries, some from the renal portals, and empties into the hepatic portal. It is possible that it is the remains of the reptilian ventral abdominal. The postcardinals have disappeared in the adults. Remnants remain in the supracardinal system and in the renal portals, which originated as detached parts of the embryonic postcardinals.

Mammals

The mammalian venous system (Fig. 261) is rather simple in plan but not in detail. The complete division of the heart into two separate halves has made a decided change in the return of the blood, and in this respect it is simpler than in the lower forms. All the blood from the head and anterior limbs comes to the right atrium through the precavae or superior venae cavae, which may be paired or single. The jugulars and the subclavians unite, forming innominate veins emptying into the precavae. The precavae have the same origin as in the reptiles. In many mammals the blood from each side of the head and from each fore limb returns separately through the original two precavae. In others, as in man, the left precava has disappeared and the left innominate vein has passed over and joined the right precava; only the coronary sinus remains as a vestige of the left precava.

The postcava carries all the blood from the posterior part of the body and empties into the right atrium. As in the reptiles, the sinus venosus has disappeared, having been incorporated into the right atrium. All trace of the renal portal system has disappeared, and the epigastric is small and changed in function. The hepatic portal functions as it does in all vertebrates, delivering its blood to the liver, but it no longer has a connection with the iliacs or the renal portal. The blood from the liver is emptied into the postcava as this vessel passes through the liver. A large vein, the azygos, collects blood from the ribs and empties into the precava just anterior to the heart. In mammals with paired precavae, a right and a left azygos may be present. The azygos vein has been considered a remnant of the postcardinals. The posterior portion of the azygos may be derived from the anterior part of the postcardinal, but the major portion seems to be derived from the supracardinal system of reptiles. The supracardinal system includes the vertebral veins of reptiles and birds and is formed from the union of segmental branches of the postcardinals.

A history of the venous system carried through the vertebrate classes shows that, from a paired, symmetrical structure in the fishes, there has

been a gradual shift to the right side of the body and the development of an asymmetrical system. The shift is complete in birds and mammals. The system has followed all the changes of the heart and has simplified its plan as the gills disappeared. As structures drop out and functions change, the vessels either find other territory to draw from or

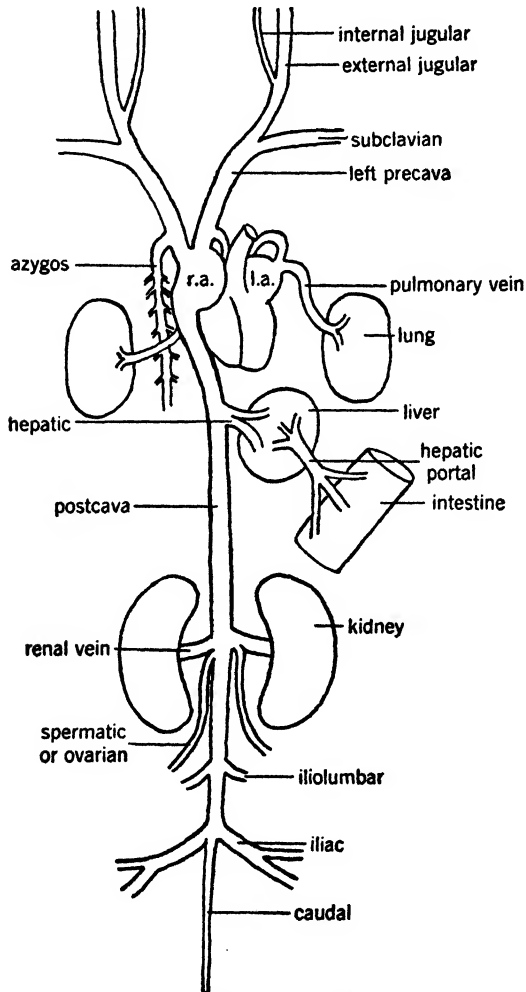


FIG. 261. Diagram of the venous system of a mammal (ventral aspect).

become vestigial and finally disappear. There is much variation within the placentals, and some striking conditions of the veins in marsupials and the monotremes suggest traces of reptilian ancestry. There have been so many changes in the system at the different levels of vertebrate history that the story of any individual part becomes enormously in-

volved by the time the placentals are reached. Developmental studies, though helpful, often fail to show clearly what has happened in the past. The history of the composite blood vessels will always be an interesting problem for biologists.

Lymphatic System

The lymphatic system is a set of vessels and associated structures that collect the lymph from various parts of the body and return it to the circulatory system. The lymph consists of that part of the blood which is continually leaking out of the capillaries into the intercellular spaces and the body cavities. It bathes the individual cells, carrying

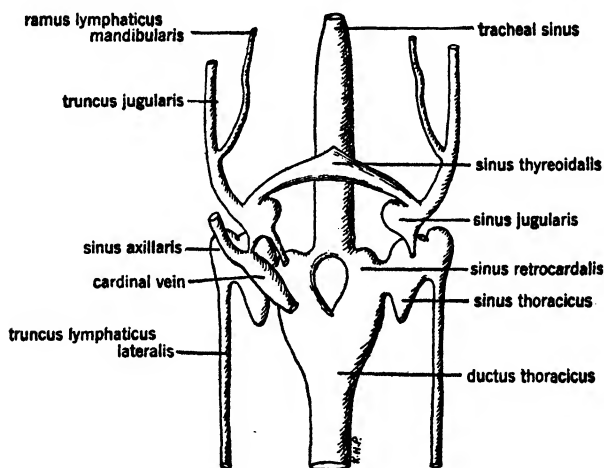


FIG. 262. Schema of the lymph sinuses of a lizard (*Lacerta vivipara*). After Hoyer.

food to them and removing waste. Lymph is made up chiefly of the plasma minus some of the fibrinogen and some leucocytes. Failure to restore this lymph results in an edema. The lymphatic system is an open system as it consists of sinuses as well as vessels. Lymph nodes or glands are distributed along the major vessels.

The lymphatic system was first observed about 1627 by an Italian named Aselli, who saw the prominent vessels in the mesenteries of a dog and assumed that they were lacteal veins, carrying material to the liver. Later in the century, this mistake was corrected and their true nature was established. The system has never been fully understood, and even today there is little agreement on its origin. One school has shown from its researches that the lymphatic system is an outgrowth from the venous system; another group has shown that the system is an ingrowth that develops and finally makes its connections with the venous system. Regardless of its developmental

history, it is safe to assume that, at all times, in vertebrates, the lymphatic system has been an integral part of the circulatory system. The history shows that there have been numerous changes in detail but that the system continues to perform the same function in all vertebrates.

Lymph Ducts

The function of the lymphatic system is not only to collect the lymph, but to purify it, and to return it to the blood stream. The main return of the whole lymph stream in mammals is through a pair

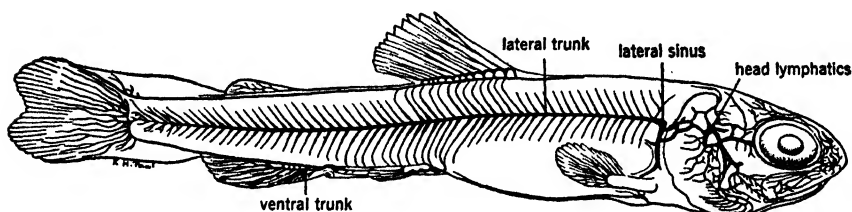


FIG. 263. Lymph system of an embryo trout. After Hoyer and Michalski.

of thoracic ducts that enter the venous system through or close to the base of the jugulars where the pressure is low. These ducts are well provided with valves, and when full they show a constriction at each valve. In man the left duct is usually the main functional duct, and the right is vestigial. The lymph ducts of lower vertebrates may empty at several points into other veins. The lymph ducts are much

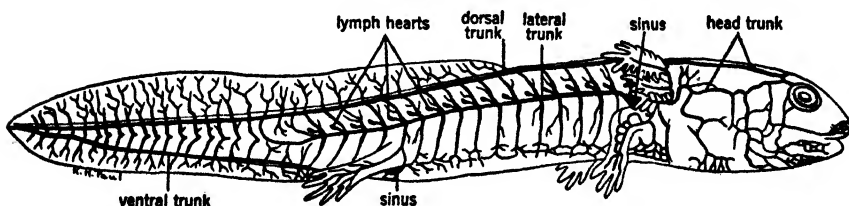


FIG. 264. Lymphatics of a salamander larva. After Hoyer and Udziela.

lighter than veins but have a similar structure. Valves to prevent backflow are scattered throughout the vessels. Stomata opening into the coelom have been described in the mesenteries of man and other animals.

Lymph vessels occur in all vertebrates. The lymph vessels of fishes that have been studied show an extensive superficial series of lymph vessels, along the sides of the body and extending into the tail and fins (Fig. 263). In the body cavity, the lymph ducts parallel some-

what those of the major blood vessels. Instead of one main entrance into the venous system as in mammals, there are several openings, at the anterior, middle, and posterior ends of the body. Amphibians have a lymphatic system resembling that of the fishes. Lymph sinuses are well developed in the amphibians, especially in the Anura. These are large spaces under the skin, in the mesenteries, and in many other parts of the body, draining into the lymph ducts. Lymph sinuses occur in all the higher vertebrates.

Lymph

The lymph is colorless and has some clotting ability, but not as much as the blood from which it originates. Leucocytes are commonly found in the lymph but erythrocytes are ordinarily absent. The amount

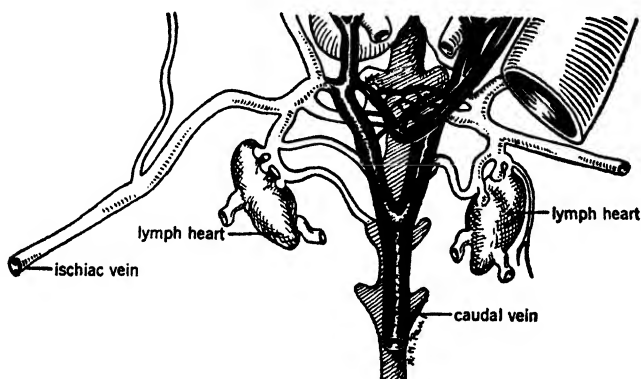


Fig. 265. Lymph hearts of an alligator. After Spanner.

of medium passing through the lymphatic system is much smaller than that of the blood-vascular system, and its movement is much slower. Its movement in birds and mammals depends on pressure from general muscular activity of the body. Some pressure is exerted by the blood through the capillaries, forcing the lymph to move along. In lower vertebrates pulsating lymph hearts force the lymph from the ducts into the veins. Lymph hearts appear in some fishes and are present in amphibians and reptiles. The urodeles generally have a pair of posterior lymph hearts, but the Anura have two pairs, a posterior pair in the region of the iliacs and an anterior pair near the ventral branch of the jugular. Reptiles retain only a posterior pair of lymph hearts connecting with the iliacs (Fig. 265).

Lymph Nodes

Lymphoid tissue occurs in all vertebrates and in the higher vertebrates is organized into units known as lymph nodes. These appear

first in the reptiles and are present in birds and mammals. These nodes are scattered in all parts of the body, ranging in size from that of a pinhead to that of a bean. They are supplied with an artery and a vein. An afferent lymph vessel carries lymph into the sinusoids of the node and efferent vessels drain the lymph from the node. In the node the lymph is filtered of bacteria and other foreign substances that it has picked up. When bacteria become too plentiful the nodes swell and may break down and abscess. A type of leucocyte known as lymphocytes is formed in the nodes. In the mammals the nodes are numerous in the axilla, groin, neck region, and throughout the body cavity, so that practically every system and organ is well supplied except the deep parts of the central nervous system, the bone marrow, and a few other structures. The haemolymph glands, associated with the carotids and some of the large veins, are not glandular in structure and differ from lymph nodes in containing red corpuscles.

Both the palatine and pharyngeal tonsils are masses of lymphoid tissue and function as lymph glands. The tonsils of the palate are oval bodies imbedded in the walls of the upper pharynx. They have numerous pits and depressions and a series of complicated crypts around which the lymph vessels are grouped. The pharyngeal tonsils are posterior to the Eustachean tubes and along the roof of the pharyngeal cavity. Isolated follicles of lymphatic tissue appear in the intestine of the lower vertebrates, but in reptiles, birds, and mammals they form large structures in the wall of the small intestine and sometimes in the large intestine and are known as Peyer's patches.

In a horse these may be an inch or more wide and fifteen inches long. The pancreas of Asellus is a very large lymph gland in the center of the dorsal mesenteries of mammals.

The largest and most prominent lymph node is the spleen, a dark colored structure lying close to the stomach and present in all vertebrates above the cyclostomes. It is highly vascular, being well supplied with arteries and veins, and is made up of spleen pulp covering a trabecular network so that it can fill and empty rapidly. It has various circulatory functions, serving as a blood reservoir and as the origin of lymphocytes. If it is removed, the body seems to have lost some of its protection against infections. In certain infections such as malaria, the spleen becomes greatly enlarged.

CHAPTER THIRTEEN

Respiratory System

Because of thick body walls and impervious coverings, such as scales, dermal plates, feathers, or other integumental materials, all vertebrates require some special means of respiration for supplying oxygen and removing carbon dioxide. In land animals this process is carried on through moist membranes of the lungs or other parts of the body. The gills of fishes are composed of lamellae in which the blood is exposed to the water through a thin membrane that permits an interchange of gases. Some fishes, such as the climbing perch (*Anabas scandens* and *Saccobranchus*), have accessory gill chambers with additional respiratory surfaces, so that they can remain out of water for some time.

Swim Bladder

One of the most striking features of fishes is the peculiar swim bladder, an airsac present in all fishes except the elasmobranchs and a few bottom feeders, such as flounders (Pleuronectidae), where it is lost in the adult stage although present in the young (Fig. 266). There is no definite trace of the swim bladder in the elasmobranchs, although some investigators have thought that they observed it. The swim bladder is a large thin-walled sac lying in the body cavity, dorsal to the stomach; it is filled with oxygen, nitrogen, and carbon dioxide in varying proportions. It originates as a diverticulum on the ventral side of the digestive tube in *Polypterus* (Fig. 266 D), laterally in the Dipnoi, and dorsally or dorsolaterally in the teleosts (Fig. 266 A), and may be single, double, ventral, lateral, or dorsal. Several theories have been proposed to explain the origin of the swim bladder. Goodrich suggests that perhaps the most promising is that of Spengler, who thought that the swim bladder might be derived from a posterior pair of gill pouches. The migration of these would account for most of the positions of the swim bladder found in fishes.

Swim Bladder of Intermediate Fishes

Many fishes can use the swim bladder as a lung. The most lung-like swim bladders are found in the intermediate fishes, where the

structure is usually long, much more than a simple sac, and connected to the throat region by a large-mouthed duct. *Amia*, *Lepisosteus*, *Acipenser*, *Polyodon*, *Polypterus*, and the Dipnoi (Fig. 266) all have large, prominent swim bladders that structurally very much resemble simple lungs, since they have a large blood supply and also red bodies and gas glands. These gas glands consist of an epithelial layer and an underlying rete mirabile of blood vessels, forming a blood net close to the surface, so that there can be an exchange of oxygen. *Polypterus* has a double sac; *Amia* and *Lepisosteus* have single ones. These bladders are very important accessory organs of respiration in these fishes. *Amia* and the gars (*Lepisosteus*) frequently come to the surface to gulp in fresh air. They can live in water that is practically devoid of oxygen. Gars, when caught in nets, are generally found dead because they cannot survive being held under the water for a long period. The Australian lungfish *Neoceratodus* lives in waters that become stagnant; the African lungfish *Protopterus* lives in waters that dry up periodically. At the beginning of the dry season, *Protopterus* burrows down in the mud, forms a slimy cocoon, and remains there until the next flood water, connected with the surface by a small tunnel through which it breathes. These cocoons, with their living contents, are now shipped all over the world.

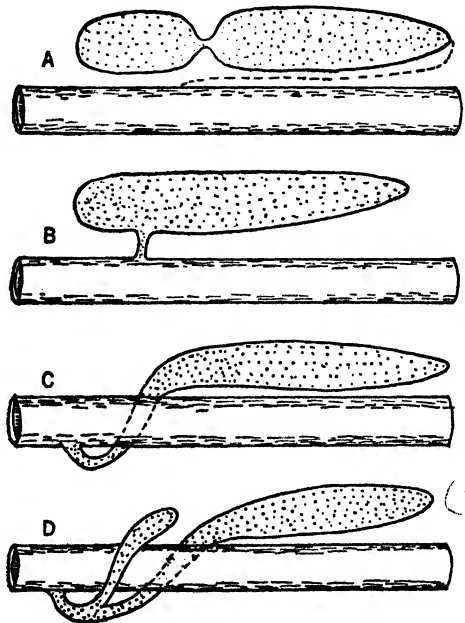


FIG. 266. Diagrams of swim bladders in fishes. A, teleost with a closed duct; B, *Lepisosteus*, open duct; C, *Neoceratodus*, open duct; D, *Polypterus*, open duct. After Kerr and Goodrich.

Swim Bladder of Teleosts

The teleost swim bladders are of two types: those in which the pneumatic duct is permanently closed (physoclisti) (Fig. 266 A); and those in which the pneumatic duct is open (physostomi) (Fig. 266 B). Those with the open duct can change the air quickly by gulp-

ing a fresh supply at the surface, but those with the closed duct regulate the density of the enclosed gas slowly. The sac itself may be single or may be constricted to form a double- or a triple-chambered structure. The herring, a rather primitive teleost, has a second duct that opens out near the anus.

The blood supply of the swim bladder comes from the sixth arterial arch in *Amia*, *Polypterus*, and the Dipnoi, whereas it comes from the dorsal aorta in the teleosts. Blood is returned directly to the heart only in the Dipnoi. The innervation is through the vagus nerve and the autonomic system.

Although originally an organ of respiration, the swim bladder has developed other uses that make it an important fish structure. In the intermediate fishes, it seems to be chiefly an accessory organ of respiration; but in the physoclistic teleosts and to some extent in the physostomic teleosts, it serves as a reservoir of oxygen and as a hydrostatic organ regulating buoyancy. The teleost swim bladder has gas glands that separate the oxygen from the blood. Nitrogen and carbon dioxide also pass into the swim bladder. In fishes that have died of asphyxiation, the oxygen of the swim bladder has been almost entirely replaced by carbon dioxide. The anterior region of the bladder is specialized for the secretion of gases, and the posterior part for the absorption of gases, so that oxygen can be taken back into the blood when the necessity arises.

The use of the swim bladder as a hydrostatic organ is shown by experiments in which a fish is sealed in a glass bottle, with a connecting apparatus to raise and lower the atmospheric pressure. A fish adjusted to a definite pressure can remain at one level with no effort at all, but it becomes out of balance when the pressure is raised and is seen to use the fins to keep at a desired level. This effort continues until the gas pressure of the swim bladder can be changed and adjusted to this particular pressure. This adjustment is fairly rapid, even in fishes with a closed pneumatic duct. Some teleosts make a noise by vibrating their swim bladders. A connection of the teleost swim bladder with the skull by means of a chain of bones may add another function. Some think that this connection may allow the bladder to function as a pressure gauge or manometer registering on the brain through the ear.

Weberian Ossicles

An unusual specialization of fishes is the development of a series of bones, known as Weberian ossicles, connecting the swim bladder with the skull in the region of the ear. These ossicles (Fig. 267) are

peculiar to the Ostariophysi, a group of fishes including the catfishes, carp-like fishes, characins (found in South America and Africa), and the electric eels. When discovered by Weber, they were considered true ear ossicles and given the same names, but their origin is differ-

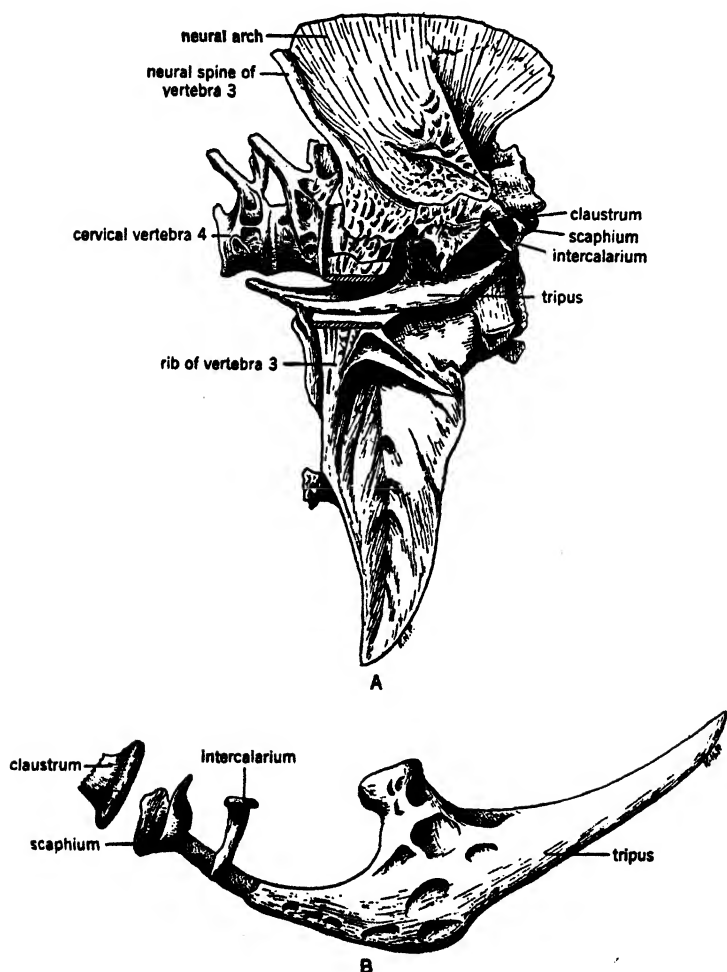


FIG. 267. Weberian ossicles of teleost, *Ictiobus urus*. A, first three vertebrae dissected to show the ossicles in position; B, the Weberian ossicles.

ent, and it is now known that they are modified parts of vertebrae. These ossicles—tripus, intercalarium, scaphium, and claustrum (Fig. 267 B)—form a mechanical structure by which the tension or relaxation of the swim bladder can be transmitted to the ear and brain. The suggestion that they may serve as a manometer may be questioned.

Gills

The function of respiration is carried on by the gills in the lower aquatic vertebrates and chiefly by lungs in the higher land vertebrates. However, other structures may aid in respiration. The ends of the alimentary canal may be vascular, as in the lungless salamanders, and serve for respiration; in amphibians, the skin is supplied with fine blood vessels and becomes an important organ of respiration, as necessary as the lungs themselves. Gills are prominent features of fishes and amphibians but do not develop in reptiles, birds, and mammals.

Gill Slits

Gill slits are present in the protochordates, although it is possible that their main function here is divided, since they are also important in food-getting, in connection with a ciliated groove, the endostyle. In *Amphioxus* they probably serve in both ways.

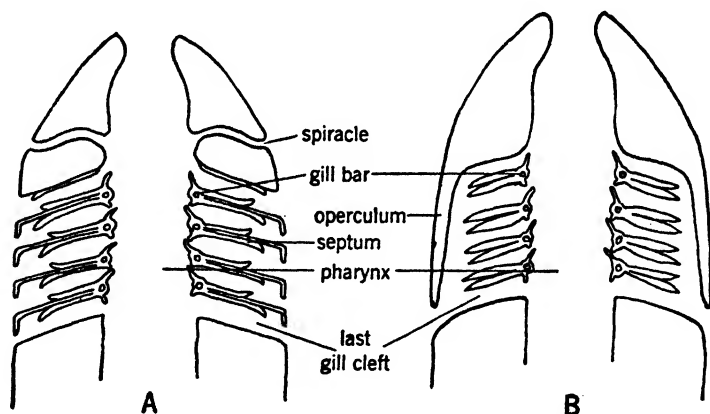


FIG. 268. Diagram showing arrangement of gills of shark (A) and teleost (B).

In the developing vertebrate embryo the endodermal pouches in the side walls of the pharynx extend to the ectodermal covering of the body wall, to which they grow fast, and become pierced by openings called gill slits. The number of gill slits is variable, with a greater number in the lower forms and a less number in the better-organized forms. *Amphioxus* has about one hundred and forty pairs, the hagfishes from seven to fourteen pairs, the lampreys seven, and two primitive sharks, *Hexanchus* and *Heptanchus*, six and seven, respectively. The normal number is five in modern fishes except the teleosts, which usually have four. In amphibians the number is reduced to four or less. The anterior gill slit is modified to form a spiracle in sharks and

some of the lower fishes but is permanently closed in the teleosts. The spiracle shows its origin by having a small rudimentary demi-branch.

The gill slits open to the outside in several ways. Cyclostomes have sac-like gill pouches, with either separate or combined ducts to the exterior. Sharks have five slits, one for each gill, with a complete septum, while the rest of the fishes have a short gill septum and a flap or bony operculum which covers the gills, forming an atrial or gill chamber (Fig. 268).

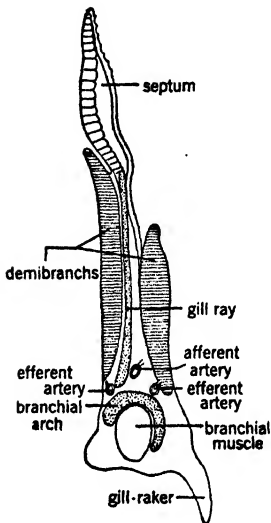


FIG. 269. Section of shark gill.

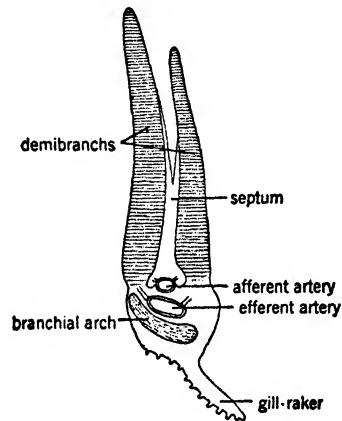


FIG. 270. Section of teleost gill.

Gill Structures

The typical gill, or holobranch, consists of a median septum, with a demibranch composed of rows of filaments or lamellae in each side, and a supporting structure of either cartilage or bone which forms the branchial arch. (See Figs. 269, 270.) The median septum is best developed in the Chondrichthyes. It becomes reduced in the intermediate fishes and completely disappears in the teleosts. Branchial rays may extend out into the gill to give it more strength and stability. The gill skeleton also furnishes a basis for the attachment of muscles, and the gills move almost constantly as the water flows over them. The lamellae on both sides have folded surfaces in which the branchial vessels with their capillaries bring the blood close to the water for the exchange of gases. The typical teleost series consists of four pairs of holobranchs, although this number may be reduced.

The internal openings of the gill chambers into the pharyngeal wall are usually protected by gill-rakers (Fig. 270), projections from the base of the gill arches, which prevent food and debris from entering the gill cavities. These rakers may be small tooth-like projections, or they may be lengthened into filamentous rays as in the paddlefishes (Fig. 271). Many teleosts have developed valves on the sides of the

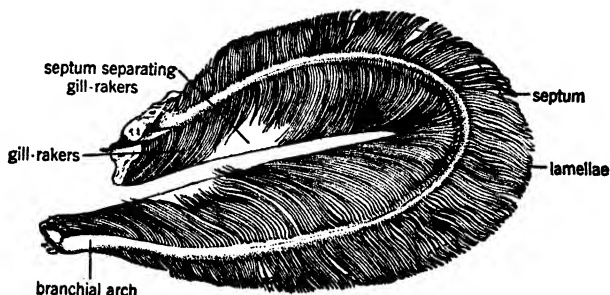


FIG. 271. Gill of paddlefish (*Polyodon spathula*) with filamentous gill rakers.

mouth which permit the flow of water inward but prevent an outflow when the mouth cavity is compressed. Water taken in through the mouth is thus forced through the internal gill openings and over the gills. Ventrally the gill region is supported by the combined bases of the hyoid and branchial arches, and open spaces in the floor may be filled in by a series of branchiostegal rays.

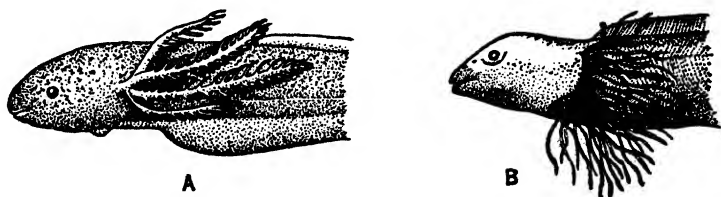


FIG. 272. A, larval ectodermal gills of *Lepidosiren paradoxa*; B, gill filaments of shark (*Gymnarchus niloticus*). After Kerr.

Besides the typical gill structures, two other types appear in vertebrates—external gills and gill filaments (Fig. 272 A, B). True external gills are found in the embryos of lungfishes and amphibians. The gills of the amphibians are of the external type, present in the developmental or tadpole stages of all, but lost in those adults that have become adapted to land life. Some water-living urodeles retain their gills for respiration in the adult stage, since the lungs are usually small, inefficient, and sometimes lost as in the lungless salamanders. In *Necturus* the three pairs of external gills form conspicuous tufts

on the side of the neck, which wave rhythmically and are very striking in a living specimen. Thin filamentous gills appear in the embryos of all sharks and in some teleosts. These thread-like gills (Fig. 272) serve in respiration but may also function in the absorption of food. The filaments extend out from the lamellae of the gills and have branchial blood vessels corresponding to those in the gills themselves.

Lungs

The lung is a constant structure in all tetrapods with the single exception of a family of the Amphibia, the Plethodontidae, in which it has been lost. These lungless forms carry on respiration through the capillaries of the skin, mouth, pharynx, esophagus, and anus.

Origin of Lungs

It was indeed fortunate for the first tetrapods that they could make their approach to land with respiratory structures already supplied by their fish ancestors. In spite of the fact that both fishes and tetrapods have sac-like respiratory structures, there is some question as to the homology of these organs. One hypothesis would derive the swim bladder of the fishes from a small pouch that originates from the anterior part of the foregut; another would derive it from the posterior pair of gill pouches. The lungs of tetrapods do originate from a small pouch that develops on the ventral side of the foregut, first as a single sac, then becoming bifurcated to form the double lobes. A happy solution might derive both structures from the posterior gill pouches. Regardless of their homology, swim bladders and lungs have a number of common points: both are used for respiration; both are used in water animals to control the density of the body; both may be single or double; both are innervated by the vagus nerve; both are supplied by the sixth arterial arch (tetrapods and *Polypterus* and dipnoans of the fishes). (See Fig. 266.) In other fishes, the swim bladder may arise from the dorsal or the dorsal-lateral side. It has been suggested that possibly, in the original condition, the blood supply of each was similar, and that both were supplied by the sixth arterial arch and also from the aortic arch, but the shifting of the swim bladder posteriorly caused the breaking away from the sixth arch, so that in most fishes only the aortic branch serves as a source of supply. Although the point is open to question, it seems most probable that the lungs are derived from the swim bladder.

Knowledge of the use of the lungs is comparatively modern, since nothing could be known of the function until the chemistry and physiology were perfectly understood. A real understanding of the lungs

starts with the discovery of oxygen and its relation to combustion and oxidation. Before the lungs could function perfectly in tetrapods, a number of shifts and adjustments of a mechanical nature had to be made, and these followed slowly with the development and maturity of the tetrapods. The gulping process of the fishes was a rather uncertain means of filling the airsacs, and although the general plan was the same in the Amphibia, it was modified by a new connection between the nasal sacs and the mouth, a condition started in the Dipnoi and other members of the Choanichthyes. This was completed in the early amphibians, and, with a closing valve on the nostrils, it was possible to use the throat and pharynx to force air into the lungs, and to utilize the elasticity of the lung structure to help in expelling the air. There is a steady improvement in this process of supplying air to the lungs that follows through the reptiles and reaches its perfection in the birds and the mammals. A few reptiles have a secondary palate that pushed the posterior nares closer to the pharynx (Crocodilia).

The swim bladder of the crossopterygian, already functioning as a lung, was probably a simple sac-like structure with a rich vascular lining. This structure was inherited by the amphibians who retained the sac-like structure. Higher in the tetrapods, septa and cross septa develop in the lung, until it becomes divided into many compartments (Fig. 281) and appears filled with tissue. This internal division continues, building up the alveolar surface until in birds and mammals the inner surface is comparatively enormous, providing ample surface for the exchange of oxygen and carbon dioxide.

The lung pattern might be likened to the familiar pattern of the acinose gland, resembling a bunch of grapes, which divided and subdivided to reach eventually the bird and mammal condition. Along with this increase in complexity, many associated structures, such as trachea, bronchi or bronchial tubes, muscles for respiration, and others, develop. In the sac-like lungs of the early tetrapods the trachea or windpipe divides into short bronchial tubes which extend to the anterior end of the lungs, but not into them at all; but, as the septa and cross septa add to the complexity of the cavity, the bronchial tubes extend farther into the lungs. Most reptilian bronchial tubes are rather short and simple, but in the crocodiles the bronchial tubes begin to make quite an extension into the lungs.

Birds have a complicated bronchial structure, and the maximum is reached in the mammals, where the bronchus, with its cartilaginous supports, forms a finely subdivided tree, the smaller ends or twigs not having cartilaginous supports but being finely subdivided to reach the alveoli. One of the best pictures of the mammalian lung is obtained by injecting the bronchial tree, arteries and veins, with celluloid of

different colors, and corroding away the tissues with acid. This gives a negative of the lung structure that is very instructive. Lungs dried under pressure of compressed air show the outside form in a very pleasing manner. These must be thoroughly dried and poisoned to keep away insect and mammalian pests. The lung is supplied with an extensive series of lymphatic vessels that extend to every part of the lung tissue. The innervation is through the pulmonary branches of vagus and the autonomic system, which together form plexuses that supply the lung. The arteries from the aorta extend into the lung tissue and supply the nourishment needed.

Trachea

The trachea, slightly more than a simple duct in amphibians, becomes a tube reinforced with cartilage in the higher tetrapods, preventing collapse. The trachea connects the lungs to the pharyngeal cavity, and in higher vertebrates, splits at the lower end into bronchi, bronchioles, and finer subdivisions which enter the tissue of the lung. The pharyngeal opening, the glottis, is a mere slit at first but comes to be associated with a specialized structure, the larynx, in the higher tetrapods. In the amphibians there are two small cartilages on the sides of the glottis and a few unorganized pieces scattered along the length of the trachea. The reptilian trachea (Fig. 278) becomes completely ringed along its entire length, the circles of cartilage being complete in the lizards and some snakes, but in others the dorsal side is of softer cartilage or with an incomplete circle so that it may fit snugly against the esophagus and permit an easier passage of food along the digestive tube.

Birds, with their elongated necks, have a long trachea (Fig. 280), strengthened along its entire length by cartilaginous rings, that may become ossified. The trachea of cranes and swans is folded and coiled in the keel of the sternum, getting into the sternum during embryonic development. Birds develop the syrinx, a structure on the lower end of the trachea, between the lungs. This is the sound-production organ. The syrinx consists of an enlarged chamber, formed of cartilage, with a median bar supporting a semilunar membrane, whose vibrations produce the sound. The bird larynx is but little developed. In mammals the trachea is variable, long in the giraffe and very short in the whales and sirenians, where it bifurcates just posterior to the cricoid cartilage of the larynx. Its lower end divides into bronchi, which subdivide into bronchioles and then smaller ducts which enter the structural units of the lung. The larger subdivisions have cartilaginous supports, but the bronchioles and smaller tubes do not (Fig. 282).

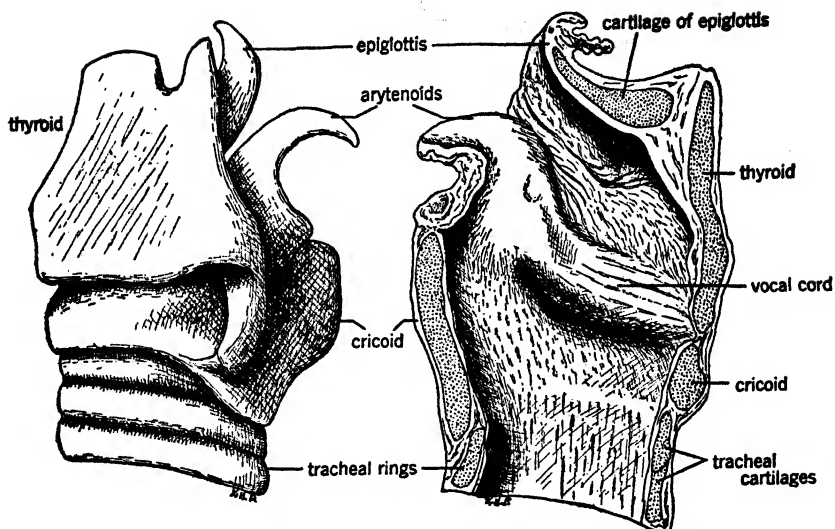


FIG. 273. Larynx of cow. A, lateral; B, sagittal section.

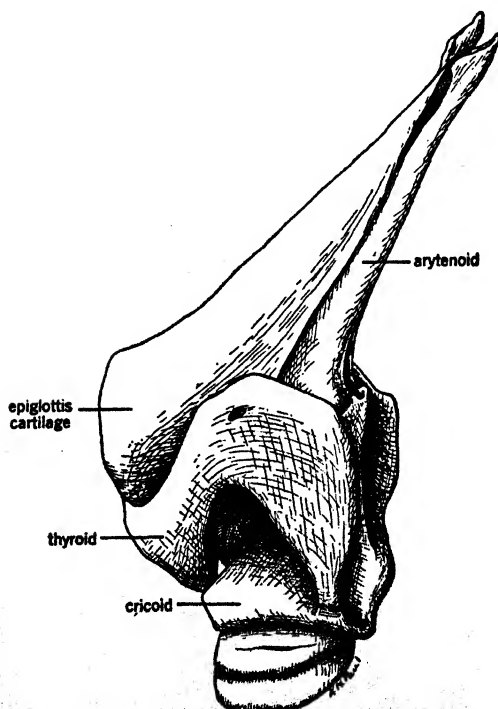


FIG. 274. Larynx of a cetacean (*Ziphius*?).

Larynx

The pharyngeal opening, the glottis, which is simple in the amphibians, becomes much more specialized as the higher groups are reached. Reptiles have a well-developed hyoid structure which helps hold the larynx in position. The reptilian larynx is formed by two arytenoid cartilages and a cricoid. The bird larynx is simple and a second organ for sound production, the syrinx (Fig. 280) is developed. The larynx reaches its greatest development in mammals (Figs. 273, 274), where it is a highly specialized sound-producing organ, with a highly developed musculature. The epiglottis, a mammalian structure, consists of a supporting cartilage, covered with mucous membrane, to

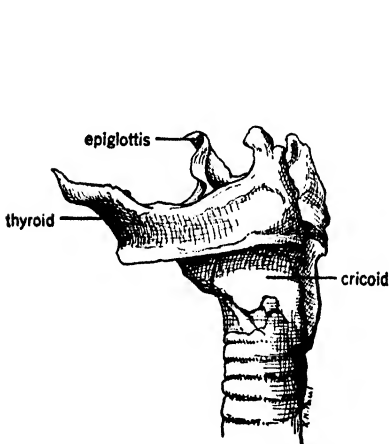


FIG. 275. Larynx of opossum (*Didelphis virginiana*).

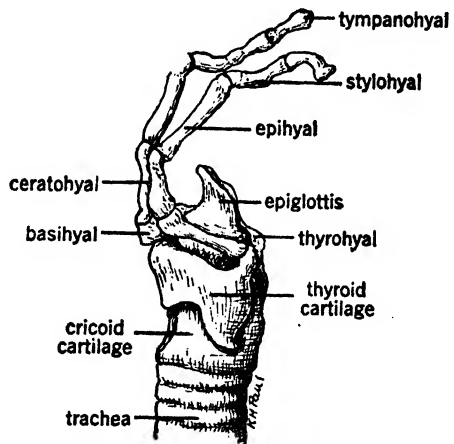


FIG. 276. Larynx of a dog with hyoid structure, from the left side. Orig.

form a ventral flap that extends back over the glottis during swallowing but is erect during breathing. Two arytenoids and two cricoid cartilages form the walls, and the thyroid cartilage forms the ventral side. (See Figs. 273, 274, 276.) The thyroid cartilage is double in the developmental stage but single in the adult. Besides these cartilages, two other pairs may be present, the corniculate cartilages at the tips of the arytenoids, and a small pair of cuneiform cartilages anterior to the corniculates.

Lungs of Various Tetrapods

Amphibian Lungs

The lungs of the Amphibia are quite variable, being sac-like in the forms that remain in water and having mainly hydrostatic function,

but becoming more alveolar in those that spend most of their time on land. The lung of *Necturus* (Fig. 281) is thin, poorly vascularized, and mainly hydrostatic in function. A *Necturus* with a total length of 270 millimeters has lungs 77 millimeters in length and of small diameter. *Ambystoma*, with a total length of 150 millimeters, has a lung 35 millimeters long, of much better quality, and with good vascular system. *Amphiuma* with a length of 770 millimeters has a right lung

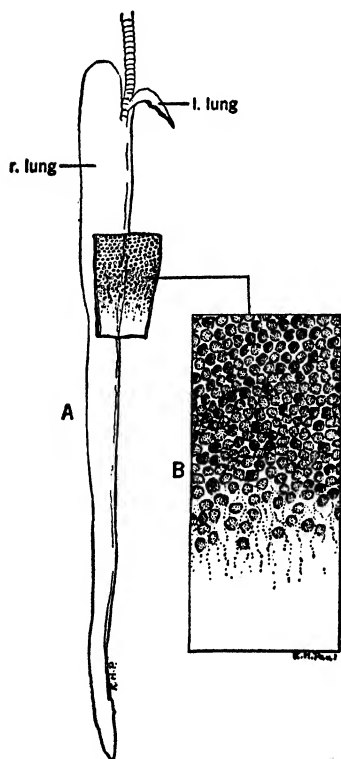


FIG. 277. A, lung of water snake, *Natrix*, anterior aspect; B, enlarged portion of lung to show alveolar structure.

550 millimeters in length and a left 410 millimeters. In both *Siren* and *Amphiuma*, the lung is approximately as long as the body cavity. The lung of the Anura, in contrast to those of the Urodela, is not greatly elongated, is of much better quality, with more alveolar spaces, and with a better blood supply. The anurans are also better equipped to force the air into the lungs by more highly developed skeletal and throat-muscle structures. The hairy frog of Africa with its hair-like development on the epidermis has added this to its cutaneous system, according to Noble. No amphibian has lungs large enough to carry on all the necessary work of respiration, and the cutaneous system supplements this work and gives the additional surface necessary.

Reptilian Lungs

The lungs of reptiles are of a higher type than those of the amphibians. (See Figs. 277, 278, 279.) Because of the presence of scales and plates, a cutaneous system would be worthless to most reptiles, except to a few with smooth

skins that live in the water. There is a tendency for the lungs of the lower reptiles to have a more or less barren region at the posterior end, similar to that of the lower amphibians. In chameleons, this is prolonged into small airsacs, somewhat like those of birds. The breathing action is improved by a better development of the accessory structures such as the larynx, a trachea with cartilaginous rings, ribs and a body musculature that aid in respiration, a better nasal passage, and a better musculature of the mouth and throat. The lungs are free

in the body cavity, as in amphibians, and there are no pleural sacs. The simplest lungs are those of lizards and snakes (Fig. 277), in which

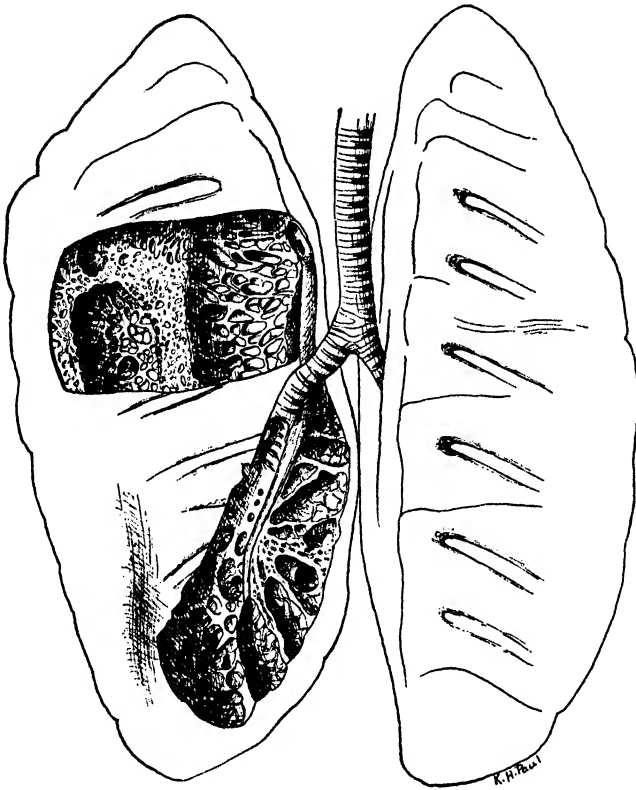


FIG. 278. Lung of Mississippi alligator, posterior view to show organization of the septa, and distribution of the bronchi. After H. Marcus.



FIG. 279. Section of lung of snapping turtle, *Chelydra serpentina*, to show alveolar structure.

the septa are not highly specialized and the bronchial tree not developed, since it just connects with the lungs and does not extend down into

them. These lower reptile lungs are not much of an improvement over those of the best amphibians. Those of snakes are greatly elongated, and the development of septa is slight. Snakes (Fig. 277) usually have the left lung reduced or vestigial. The best reptile lungs are those of the turtles and crocodiles (Figs. 278, 279), and these approach the mammalian types in the fine subdivision of the septa and the bronchial tree. The lungs of reptiles have a much better blood supply, since there is little possibility of assistance from a cutaneous source, the blood supply approaching that of the mammal in quantity. It is highly probable that some of the ancient reptiles such as the pterodactyls and dinosaurs had lungs of a very advanced type.

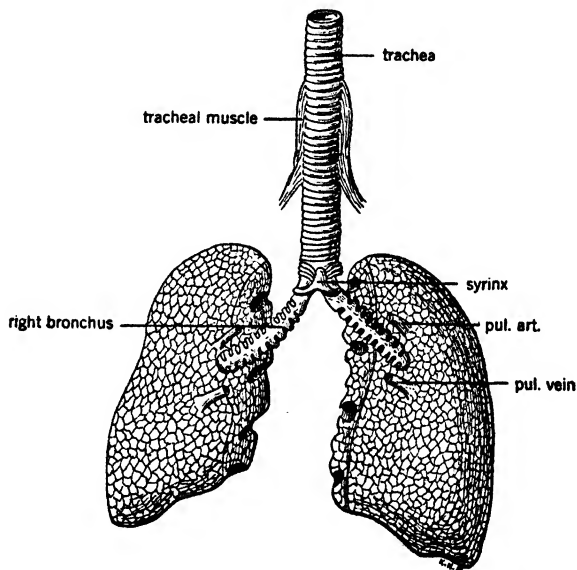


FIG. 280. Lungs and trachea of a chicken (airsacs omitted).

Bird Lungs

Birds have an extremely efficient respiratory system (Figs. 280, 281) which gives them a greater oxygen supply and enables them to live at a high tension. The lungs are filled with septa and appear sponge-like in section. The respiratory area per pound of body weight is consequently very high. Two features stand out distinctly in the lungs of birds: the development of the airsacs and the peculiar division of the bronchial tubes. The accessory airsacs, which extend the lungs to practically all parts of the body, are supplied with arterial blood and appear to have pneumatic functions, as well as those associated with respiration. One pair of sacs enters the long bones of the wing,

making them pneumatic. The pneumaticity varies within the class, but generally the best fliers have the best development of these sacs. The connection with the skeleton is sufficient to permit breathing through one of the long bones if it is broken open and the trachea is tied. The bronchi bifurcate and enter the lung, forming secondary bronchi, which in turn give off a series of tubes that retain about the same diameter throughout. The bronchi and some of the tubes open into the airsacs, so that there are no blind passages in the lungs of birds.

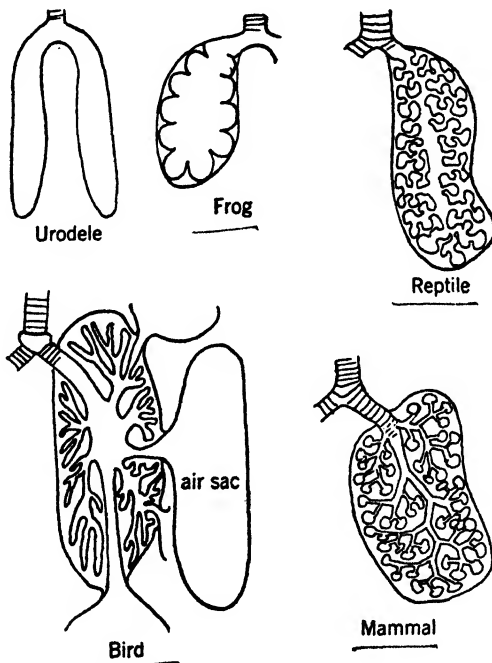


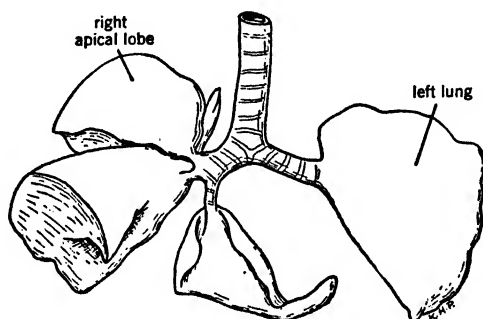
Fig. 281. Diagrams showing internal structure of lungs.

The accessory airsacs usually consist of six pairs: a cervical pair at the base of the neck; a clavicular pair in the region of the clavicle; three pairs connected with the abdominal cavity, anterior, intermediate, and posterior; and a small pair in the axilla. These are connected with the bronchi so that they get a direct supply of air, and the lungs have all the respired air taken out at every breath. It is probable that these sacs have an important function in keeping up the high temperature as well as assisting in respiration. The sacs themselves are not concerned in the aeration of the blood, since they have no capillaries, but act indirectly in the exchange of air in the lungs. The airsacs make the body pneumatic, preserve heat, lessen the friction between flight

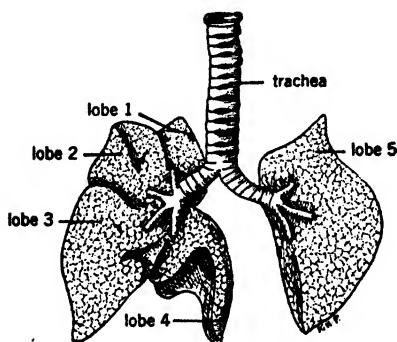
muscles, and assist in respiration by making possible a complete change of air in the lungs at every breath. The diaphragm is incomplete and of small value in changing the air in the lungs, but the skeletal parts are in such close connection with the lungs and accessory sacs that any movements of the body, particularly those of flight, assist in moving the air.

Mammalian Lungs

The lungs of mammals (Figs. 281, 282, 283), like those of birds, are sponge-like in appearance. They are enclosed in pleural sacs and are suspended in the pleural cavity and are separated by the medias-



A. Lung of *Echidna*. After H. Marcus.



B. Lungs and trachea of white rat.

FIG. 282. Mammalian lungs.

tinum enclosing the heart. They are separated from the rest of the body cavity by the dome-shaped diaphragm. Inhalation and exhalation are carried on by means of movements of the ribs, intercostal muscles, sternum, and the muscular diaphragm, by which the capacity of the chest cavity is increased and diminished. The abdominal muscles also play a prominent part in the process. The air is conducted to the

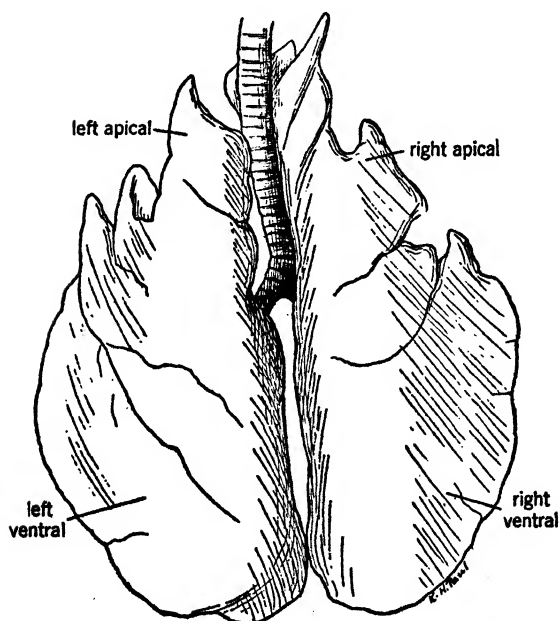
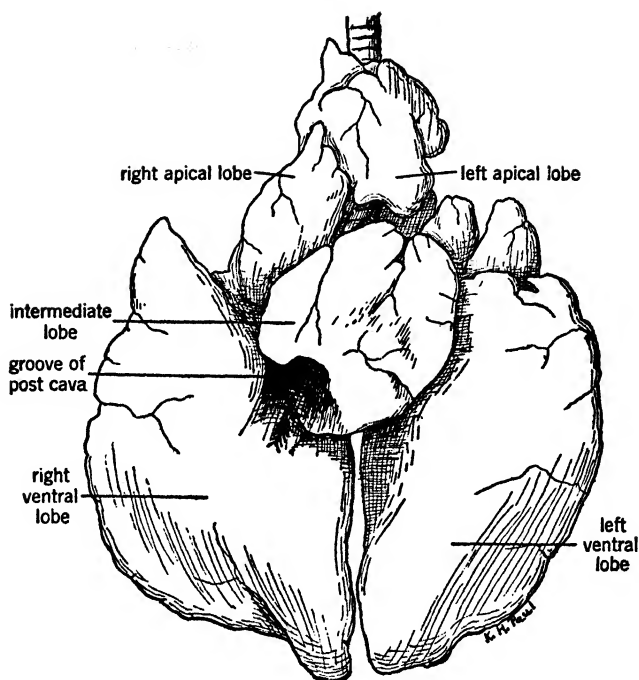


FIG. 283. Lung of an ox, ventral aspect; dorsal aspect.

lungs through the nasal cavity and pharynx, to the glottis. The trachea, extending down into the lungs, bifurcates before entering. On entering the lungs, the bronchi, usually two in number, divide and subdivide until they become small tubes, still protected by rings of cartilage. The bronchioles or final conducting tubules are without cartilage. The bronchioles connect with the infundibula and the areas where the alveoli are to do their work. In this way, every part of the mammalian lung is connected with the bronchial tree. The cartilage of the bronchial system becomes progressively less organized, until in the final divisions the cartilages are slightly connected plates. The alveoli of the infundibula are lined with moist epithelium, laced with capillaries, and through these the interchange of gases takes place. The respiratory centers of the brain control the lung action, keeping the carbon dioxide at a definite level. The lungs are extremely elastic and can be expanded several times their normal size without breaking. There is a considerable amount of cartilage, practically all of which is in connection with the bronchi, and smooth muscles which wrap around them forming a latticework. The pulmonary arteries, coursing along the bronchi, extend to the limits of the lung and supply the blood that is to extend into the alveoli. Coursing along the bronchi also are corresponding veins, which pick up the blood after it has been through the alveoli and return it to the heart. As mentioned before, the main innervation is through the pulmonary branch of the vagus and the branches from the autonomic system.

There is considerable variation in the lungs of mammals, since the formation of the lobes may be somewhat different in the same species. Since the heart tilts to the left side, there is always a difference between the right and left lobes, both in number and size.

CHAPTER FOURTEEN

Urogenital System

The nitrogenous wastes of the body, consisting of salts and the end products of protein metabolism, must find a way out of the blood stream other than by means of respiration and perspiration. Some type of excretory organ is necessary for this function. Nephridial tubes perform this function in some invertebrates, and similar structures, forming the excretory part of the urogenital system, dispose of the nitrogenous waste in the vertebrates. The urogenital system of the vertebrates consists of two systems, inseparably united: one, the excretory, and the other, the reproductive system. They use the same ducts and hence are treated as one system. It is assumed that originally each system had its own outlets to the exterior but that development and changes of structure in the vertebrate body caused their combination and thus reduced the number of ducts and openings into the body cavity. The reproductive organs are concerned in the production of ova and spermatozoa and in getting these products out of the body or in providing a place for fertilization. The excretory organs or kidneys originated in the segmental pores and tubules of primitive chordates, in which there were direct outlets for wastes from the coelomic cavity to the exterior. In the Cephalochordata these tubules, or nephridial ducts, have ciliated openings, the nephrostomes, into the coelomic cavity, and also are associated with knots of blood vessels, so that the excretory products are taken from both the coelomic cavity and the vascular system. The sex products of *Amphioxus* are discharged into the atrial cavity and escape through the atrial pore. In the vertebrates the products of the kidneys are taken out through paired ducts, one from each organ. These ducts also carry the male reproductive cells, except in cyclostomes and some fishes.

Kidneys

The kidneys of the vertebrates are of three types, each of which probably represents parts of a long continuous structure that once extended from one end of the body cavity to the other. The pronephros or anterior kidney is functional in the developmental stages

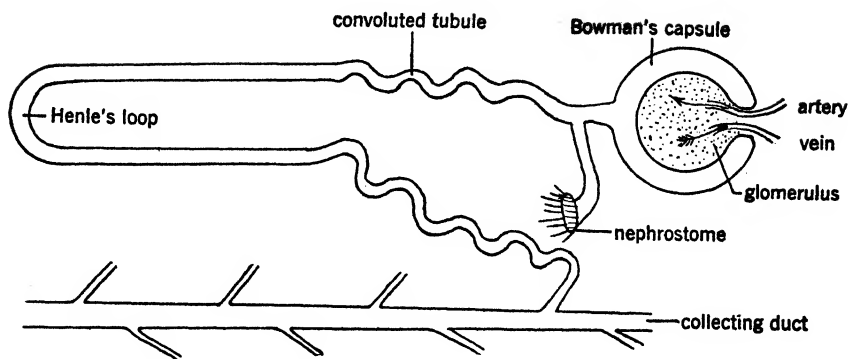
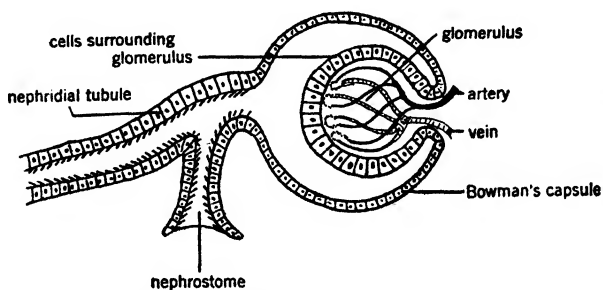
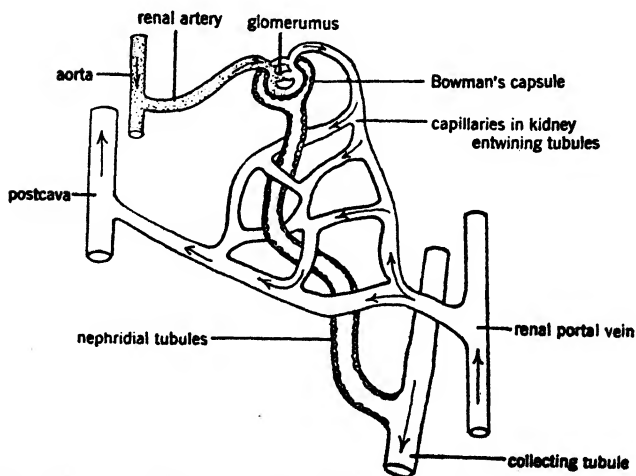


Diagram of renal unit. After Kingsley.



Malpighian body, diagrammatic. After Kingsley.



Circulation around tubules of the kidney. After Curtis and Guthrie.

FIG. 284. Structure of renal unit.

of cyclostomes and fishes but is transitory in the embryos of higher vertebrates. The *mesonephros* or middle kidney is functional in adult fishes and amphibians (Figs. 293, 294, 295). The *metanephros* or posterior kidney is the adult organ of excretion in reptiles, birds, and mammals. All kidneys develop from the *mesomere* and lie dorsal to the body cavity, so that they are covered with peritoneum, which separates them from the coelom.

The Renal Unit

The vertebrate kidneys each consist of a number of uriniferous tubules which, except in the amniote kidney, had a segmental origin, all coming from the mesodermal mesomere. In the more primitive kidneys each tubule had a peritoneal funnel or nephrostome, into the body cavity. Adjacent to this, a small mass, containing a network of capillaries, pushes out of the tubule wall and forms a glomerulus. The glomerulus becomes invaginated in the wall of the tubule, thus forming a capsule about itself known as Bowman's capsule. The entire unit composed of the glomerulus and Bowman's capsule (Fig. 284) is termed the Malpighian body or renal corpuscle. From the corpuscle, a more or less convoluted uriniferous tubule extends to unite with others and empty into the uriniferous duct (ureter) leading from the kidney. The nephrostome persists only in the kidneys of some of the lower vertebrates and is closed in all the higher vertebrates. This unit, consisting of the renal corpuscle and the uriniferous tubule, is the fundamental unit of all vertebrate kidneys.

Archinephroi

The forerunner of the vertebrate kidneys was probably the *holonephros* or *archinephros*. This is a very primitive kidney seen only in the embryo of the hagfish. It consists of numerous segmental, uriniferous tubules covering about seventy somites. Each tubule has a nephrostome and empties into a common longitudinal duct which can be called the archinephric duct. Glomeruli are present only in some of the posterior tubules. From this primitive structure, the kidneys of the higher vertebrates seem to have developed. The anterior tubules of the *archinephros* apparently become the *pronephros* in the embryo hagfish. Consequently, the hypothesis has been proposed that each of the three adult kidneys of the vertebrates are successive developments of different regions of the *archinephros*.

Pronephroi

The *pronephroi* occupy the most anterior position in the body of any of the three adult kidneys. A *pronephros* has only one pair of

tubules per somite, and consists of only a few tubules (numbering from one to thirteen), each with a glomus or knot of blood vessels. The nephrostomes provide ciliated openings into the metacoel (Fig.

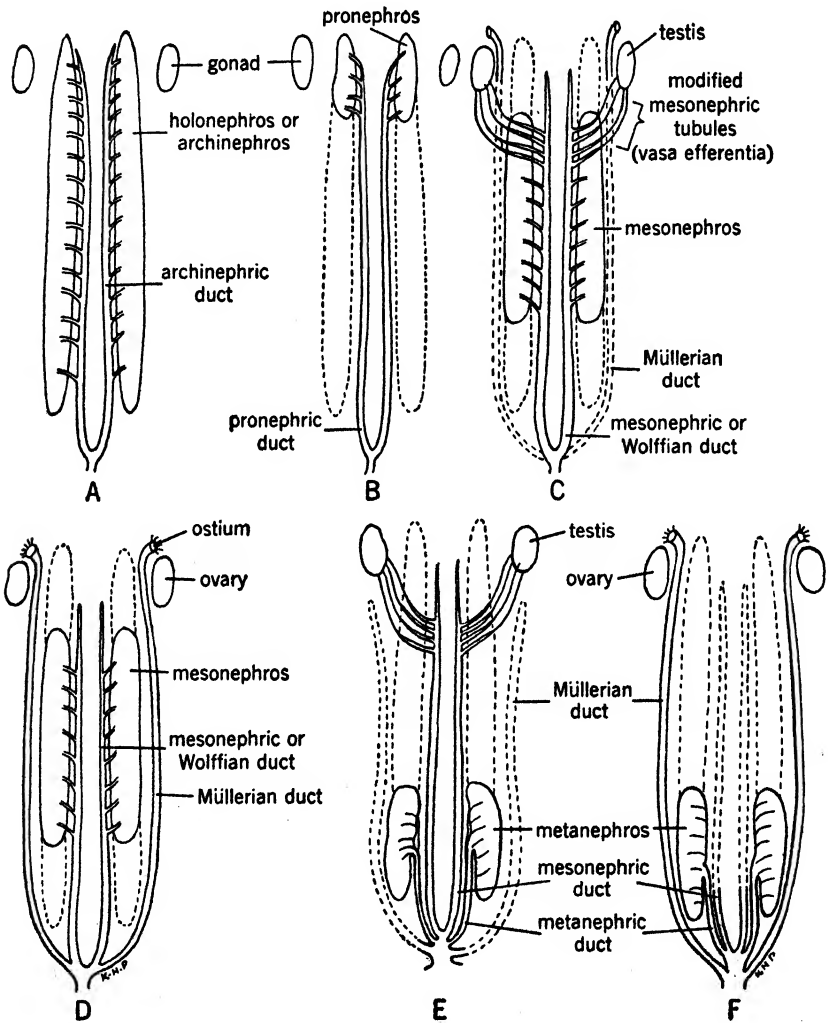


FIG. 285. Diagram showing plan of holonephric or archinephric kidney and ducts, and relations to the various types of kidneys. A, diagram of archinephroi; B, pronephroi; C, male mesonephroi; D, female mesonephroi; E, male metanephroi; F, female metanephroi.

286), and the pronephric duct collects the waste from the tubules and empties it externally. The unit of structure is quite primitive when compared with that of the metanephros, since the connection between

the glomeruli and the tubules is rather simple. The glomeruli may be external and project out through the nephrostomes into the coelom, instead of being invaginated in a Bowman's capsule. In some forms (pronephros of frog embryo) the pronephric nephrostomes are closed

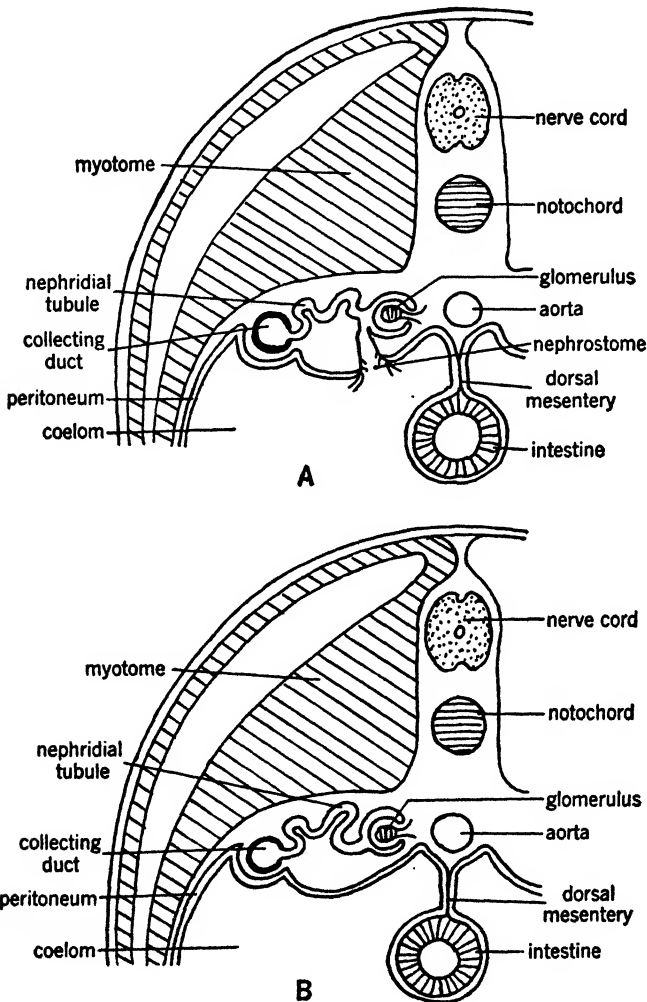


FIG. 286. Diagram showing structure of kidney. A, nephrostome present; B, nephrostome absent.

off from the coelom, forming a separate chamber that is comparable to a Bowman's capsule (Fig. 284). The blood supply comes from the aorta.

The pronephros appears as an embryonic functional kidney in cyclo-

stomes, fishes, and amphibians. In reptiles, birds, and mammals it is a non-functional, transient affair appearing in early embryonic life. It is retained as an adult kidney only in the hagfishes and in some teleosts where the mesonephros may also be present.

Hagfishes have separate head and trunk kidneys, which some claim are separate units of the pronephric kidney rather than a combination of pronephros and mesonephros. Both units are derived from the archinephros (Fig. 285). The pronephroi remain in most teleosts but degenerate into lymphoid tissue as the mesonephroi arise posteriorly. The pronephroi seem to remain functional as the anterior part of the adult kidney in those teleosts which have aglomerular mesonephroi.

Mesonephroi

The mesonephros or Wolffian body, also segmental in origin, arises posterior to the pronephros. It consists of a large number of tubules draining into a mesonephric or Wolffian duct. This kidney is the functional organ of excretion in lampreys, most adult fishes, and amphibians. In the embryos of amniotes, it appears merely as a transient functional structure, soon to be replaced by the permanent adult metanephric kidney. Functionally, it is a much better organ than the pronephros, for the tubules are much more numerous and the glomeruli are enclosed in Bowman's capsules, thus forming Malpighian bodies. (See Figs. 284, 286.) The openings into the coelom, the nephrostomes, generally persist in some Chondrichthyes, *Amia*, and urodeles but do not appear in reptiles, birds, and mammals (except in monotremes). The mesonephros receives part of its blood supply from the veins of the caudal region and hind legs, which form a renal portal system (Fig. 284). The veins break up into capillaries around the tubules and are gathered together by the venae revehentes and carried forward to the heart by the postcava. The blood supply to Bowman's capsule is through the glomerulus which takes its blood from the aorta.

In most vertebrates possessing an adult mesonephros, this kidney has grown backward in its final development, utilizing tissue that gives rise to the metanephric kidney of the higher vertebrates, until it extends the entire length of the body cavity. This adult overgrown form of the mesonephros is sometimes called an opisthonephros.

Metanephroi

The metanephros arises most posteriorly in the body cavity and is the adult kidney of reptiles, birds, and mammals (Figs. 285, 288, 296, 298). It does not show segmentation so clearly as do the more primi-

tive kidneys. The origin of this kidney is from two sources: the Wolffian duct and the kidney ridge of the mesomere. An outgrowth originates from the base of the Wolffian duct near the cloaca, and, extending anteriorly and dorsally, grows to the kidney ridge of the mesomere and receives a contribution (metanephridial tubules) from this ridge.

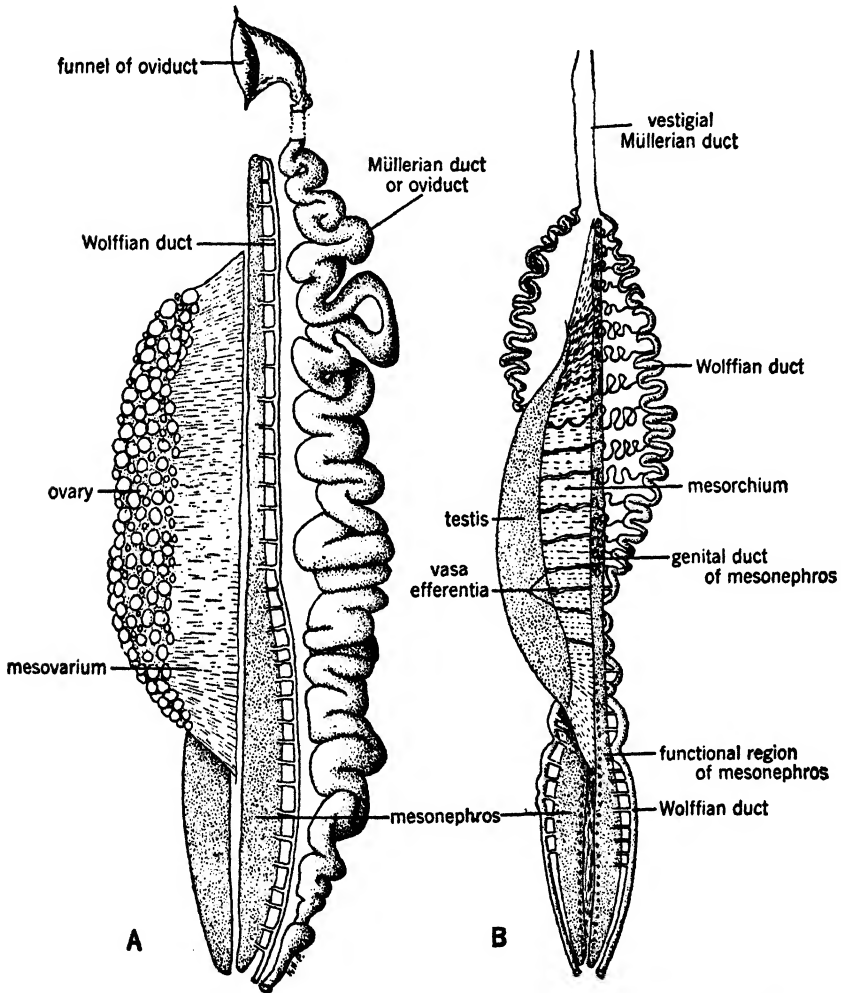


FIG. 287. Urogenital systems of urodeles. A, female; B, male. After Chase.

The new metanephric duct, the ureter (Fig. 285), is formed by the stalk of this outgrowth, which, starting at the base of the cloaca, extends forward and expands, branching in the body of the kidney, to form a series of tubes that connect with the metanephridial tubules collecting the excretions from the Malpighian corpuscles. The "pelvis"

(Fig. 288) of the kidney is an enlargement of the ureter. This new tube, which drains the kidney, has no function connected with the reproductive system. The functional unit, or renal corpuscle, remains the same as in the mesonephros, but the nephrostomes are lost and there is no connection with the coelomic cavity. The blood supply from the aorta is greater, and the renal portal system, which was intimately connected with the mesonephros, no longer supplies most of the blood to the kidney, although the veins still may pass through or over it. The kidney varies greatly in shape, being elongate in reptiles and bean-shaped in some mammals. The lobular development, although retained in young mammals, is often lost in adults (Fig. 303).

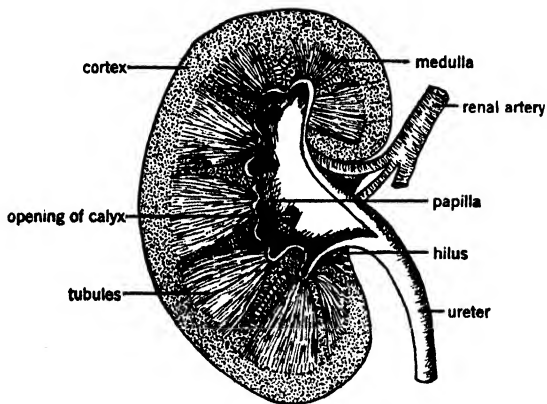


FIG. 288. Sagittal section of mammalian kidney. After Radasch.

Function. The function of the kidney is to stabilize the blood stream, by extracting water and certain protein products of metabolism, together with other salts that are constantly being added from the tissues. The organic material extracted consists of urea and its compounds, uric acid, sodium chloride, phosphates, sulfates, and a number of other salts. In abnormal conditions, sugar and albumen may be drawn through the kidneys. The failure of the kidney brings rapid death from uremic poisoning. Selective action of the cells surrounding the glomeruli extracts water and waste products from the blood (Fig. 284). The cells lining the tubules are also selective, removing and saving certain products from the solution that passes them. In certain animals of the desert, the water is reabsorbed by these cells, so that the urine is excreted as a solid.

The problem of the removal of the wastes in fishes is complicated by the differences of the media in which they live. Fishes living in salt water have an entirely different problem from those living in fresh water, although some are able to live in either salt or fresh water,

migrating back and forth for reproduction or for other reasons. Fishes living in salt water, in which the osmotic pressure of the surrounding medium is greater than that of the body fluids, tend to lose their water and to become desiccated whereas those living in fresh water with the osmotic pressure of the surrounding medium less than that of the

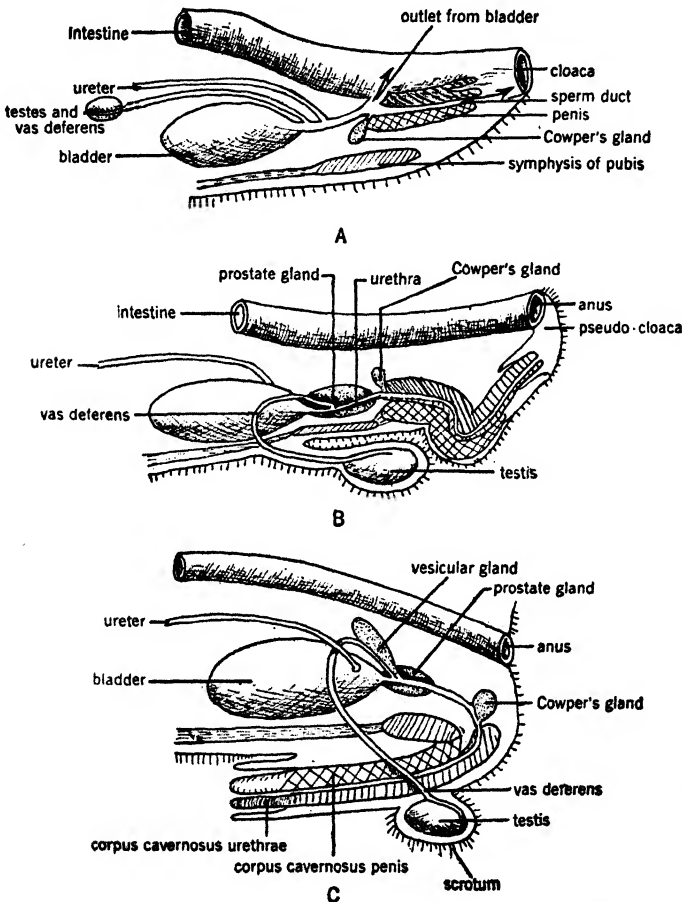


FIG. 289. Diagram of male urogenital systems in the three subclasses of the mammalia. A, monotreme (Prototheria); B, marsupial (Metatheria); C, placental (Eutheria). After Weber.

body tend to absorb water. It is clear that some sort of mechanism is necessary to permit them to maintain a constant body fluid or a concentration of materials necessary for life. According to the studies of Smith (1932) and others, the elasmobranchs appear to excrete salt through the gill membranes; furthermore they have a second mecha-

nism, which retains the urea, so that the blood becomes surcharged with it, and thus, with an increasing osmotic pressure, the organisms can excrete their wastes and not lose water. The sharks absorb water through their gills and mouth membranes and do not have to obtain water by drinking sea water. The marine teleosts, on the other hand, drink sea water and absorb both the water and its salts, excreting the excess salt through their gills. This enables them to get a water supply for their body needs. The kidneys of some marine fishes show peculiar modifications in which there is a reduction or complete absence of the glomeruli. This anatomical modification seems to make it possible for them to excrete wastes with the minimum loss of water. This subject brings up some speculations as to the origin of the fishes and seems to point to a fresh-water origin, with later migrations to the sea. Most of the beds of fossil fishes are known to be fresh-water deposits, and fossils in salt-water deposits are much less common. It seems probable that the migration of the intermediate fishes to salt water occurred sometime in the Mesozoic period, whereas the migration of the teleosts to salt water did not assume significance until some time in the Eocene, since their origin was mainly in the Cretaceous.

Adrenal Glands

The adrenal or suprarenal glands are small bodies (Figs. 296, 298, 300, 301) whose tissue is found situated close to the kidneys in all vertebrates. Although usually closely associated with the kidneys, they are important glands of internal secretion and have no relation to the kidney function. In mammals they appear as a pair of small bodies just anterior to the kidneys. They are composed of an internal medulla covered by a cortex. The medulla is derived from the sympathetic ganglia of the nervous system, and the cortex originates from the mesoderm.

Adrenal structures appear in cyclostomes as small masses of cells scattered among the blood vessels. In the elasmobranchs they appear as a small mass of cortical tissue between the kidneys and as small masses of medullary tissue imbedded in the kidneys along the segmental arteries. In amphibians, reptiles, and birds the adrenals are bodies of cortical tissue, with imbedded medullary cells, lying either imbedded or close to the kidneys.

Urogenital Ducts

The duct draining any of the vertebrate kidneys is commonly called a ureter, although it is much better to restrict this term to the duct of the metanephric kidney of reptiles, birds, and mammals. Each of

the three types of kidneys has its own duct, and these ducts are not always homologous.

Pronephric Duct

The primitive duct appearing first in all vertebrates above the hagfish is the pronephric duct draining the pronephric kidney. In the hagfish the pronephric duct appears to be derived from the earlier archinephric duct. In some cyclostomes and teleosts, where the pronephros occurs in the adult, the pronephric duct drains the kidney but does not carry reproductive products. The reproductive elements escape through pores from the body cavity in the cyclostomes and are usually carried by ducts constructed from mesenteric folds in the teleosts. The pronephric duct gives rise in several ways to the mesonephric duct.

Mesonephric Duct

The mesonephric kidney is drained by the mesonephric duct (sometimes called the Wolffian duct), which arises in the elasmobranchs from a splitting of the pronephric duct into the mesonephric duct and the Müllerian or oviduct. In other vertebrates, the pronephric duct does not split but becomes the mesonephric duct. The mesonephric duct receives the uriniferous tubules of the mesonephric kidney and carries excretory products in both sexes of the lampreys, elasmobranchs, bony fishes, and amphibians. In the males of these lower vertebrates, exclusive of the cyclostomes and teleost fishes, the duct also carries sperm as it forms a connection with the testes through the anterior uriniferous tubules, which lose their excretory function and acquire a reproductive function. The mesonephric duct is retained in the reptiles, birds, and mammals, where it functions as a vas deferens in the males and carries only sperm (Fig. 285).

In females with adult mesonephric kidneys (Fig. 294), the mesonephric duct carries excretory products only. The Müllerian duct, which splits off the pronephric duct in the elasmobranchs, becomes the oviduct. It retains a terminal pronephric nephrostome, which becomes the ostium or the funnel for receiving the eggs. In higher vertebrates, the Müllerian duct originates from the mesomere, but its development in the elasmobranchs is usually considered evidence of its phylogenetic origin. The Müllerian ducts serve as oviducts in the females of elasmobranchs, intermediate fishes, amphibians, reptiles, birds, and mammals. It frequently becomes modified into uterus, Fallopian tubes, and other structures. It does not appear in cyclostomes and teleost fishes, where other means are used for transportation of the eggs.

Metanephric Duct

The metanephric kidney, appearing in the reptiles, develops a new ureter or metanephric duct, which arises posteriorly as an outpouching off the mesonephric duct and grows forward to unite with the new kidney (Figs. 285, 297, 299, 301). In those vertebrates possessing metanephric kidneys, the mesonephric duct occurs but carries only reproductive products in the male and is non-functional and vestigial in the female. The mesonephric duct is now known as the vas deferens, and the original mesonephric tubules connecting with the testis are retained and form the epididymis.

Bladder

The urinary bladder is a variable structure not found in all vertebrates. Three types of unrelated urinary bladders occur in vertebrates. In some fishes the bladder is formed by the fused ends of the Wolffian ducts. In other fishes and in amphibians, a diverticulum from the cloaca is called a cloacal bladder, although it is independent of the ducts of the mesonephroi. Amphibia have a small ventral diverticulum which extends from the cloaca and serves as a reservoir for urine. In snakes, crocodiles, and birds, the bladder is missing, but in some of the reptiles and in all mammals it is formed from the base of the allantois. This is probably an advanced development of the cloacal bladder. In mammals the connection is direct as the ureters enter the posterior wall usually at its base.

Urethra

The duct leading from the allantoic bladder is known as the urethra. In reptiles it may be short, but in mammals it is more elongated. In male mammals, the closure of the groove of the penis further extends the urethra. The urethra carries not only the urine from the bladder but also the seminal fluid of the male (Fig. 289 C).

Reproductive Organs

The reproductive organs of the vertebrates consist of the male and female gonads, that is the testes and ovaries, with their accessory structures. There is usually a strict separation of the sexes, although cases of sex reversal are reported in some cyclostomes and fishes. Occasionally hermaphrodites appear in the vertebrates, but they are anomalies and accidental, with the exception of the myxinoidea. The myxinoidea are hermaphroditic in their younger stages, having the anterior part of the gonad female and the posterior part male. Adults

develop into males and females by the degeneration of the part of the gonad of the opposite sex.

The gonads of vertebrates are compact organs that develop the ova and spermatozoa and bring them to maturity. Both ovaries and testes are derived from the epithelium of the genital ridge of the dorsal region of the coelom, in agreement with the hypothesis that the coelom is an expanded gonadal cavity. The gonads are normally located just posterior to the kidneys, except in some male mammals where the testes may change their position and come to lie in a scrotal sac (Fig. 289), which is a continuation of the coelomic cavity.

The fertilization of eggs varies, being internal in the higher land animals and generally external in the lower water forms. Some fishes are fertilized internally, and some amphibians form a spermatophore containing a large number of spermatozoa which is taken into the cloaca of the female for fertilization. Internal fertilization generally takes place near the anterior end of the Müllerian ducts. In all classes of vertebrates each individual goes through an embryonic developmental stage in which practically all the anatomical parts of both sexes are present, but, whereas those of one sex complete their development, those of the other sex become partially obliterated and remain only as vestiges.

Ovaries

The female reproductive organs consist of the ovaries and their conducting tubes, the Müllerian ducts, or oviducts, with their modifications and accessory parts.

The ovaries, or the gonads of the female, are paired bodies, located at about the mid-region of the dorsal wall of the coelom, and lateral to the vertebral column (Figs. 293, 295, 297). Topographically they are usually close to the kidneys. They originate from the mesoderm of the genital ridge and receive primordial germ cells from the lining of the hypomere. The ovary is rather simple in structure, consisting principally of cells that are to become eggs and other cells that serve for support and nutrition.

The germinal epithelium, from which the ova arise, covers the ovary whereas in the testes it lines the tubules. Each ovum becomes invaginated and is surrounded by a number of cells which form a structure called the Graafian follicle (Fig. 290) in mammals. The oöcyte, or developing egg, is completely surrounded by cells at first, but by reorganization a follicular cavity is formed, filled with a follicular liquor. A stalk, the discus proligerus, attaches the egg, with its thin surrounding layer of cells, to the walls of the follicular cavity. No

outlet is provided for the escape of the ripe egg, and it must burst through the wall, the ruptured area forming the corpus luteum. A rich blood supply insures nutriment for the developing egg. After its escape from the ovary, it is temporarily in the body cavity and is caught or forced into the oviduct through the ostium tubae. The funnels of the two oviducts may be separate, or they may join to form a single opening as in the shark. The ducts are modified according to the type of egg developed. The large eggs of birds and reptiles must have specialized parts of the tube to supply the additional materials, so the duct is modified to supply food material, albumen, a shell membrane, and finally a shell (if one is present). Each oviduct of the mammal is modified with many different structures such as the Fallopian tube, uterus (except in monotremes), and vagina.

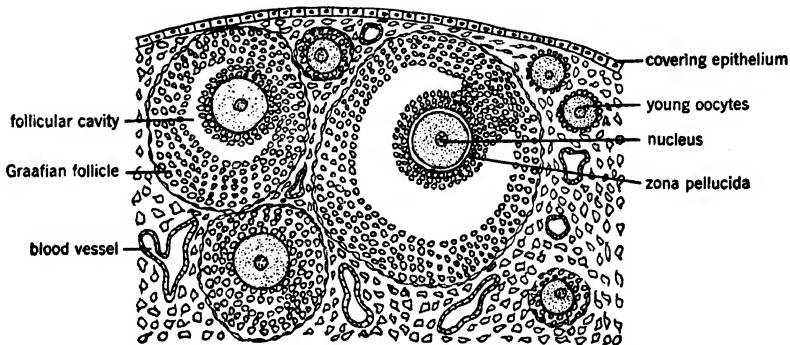


FIG. 290. Section of ovary of cat. After Jenkinson.

The ovary is held in place by mesenteric ligaments that attach it to the posterior wall of the coelom. The old ligament originally tying the mesonephros to the body wall becomes the *broad ligament*, which, with the mesovarium, holds the ovary in place. The posterior part of this old ligament forms the *round ligament*, which ties the ovary to the pelvic cavity posteriorly.

Testes

The reproductive organs of the male consist of the gonads, or testes (Fig. 285), and their accessory structures. The testes (Fig. 291) generally occupy the same relative position as the ovaries, but in some mammals they migrate seasonally or permanently to the scrotal sac, which is a diverticulum of the coelom. The testes, unlike the ovaries, are made up of a large number of seminiferous tubules lined with germinal epithelium (Fig. 291) and formed at the time of the migration of the primordial germ cells. The spermatozoa develop in the walls

of these tubules and pass through the efferent ductules or vasa efferentia into some modification of the Wolffian duct, to be stored and later discharged for the purpose of the fertilization of the eggs. The anterior part of the mesonephros loses its excretory function as the uriniferous tubules connect with the testes, forming the vasa efferentia. In *Squalus* the Wolffian duct functions partially or not at all as an excretory duct in the male, since this function is taken over by accessory ducts which drain the posterior part of the mesonephros into the urogenital sinus. In the higher vertebrates the vasa efferentia are greatly lengthened and much coiled, forming the structure called the epididymus. In the amniotes, with the development of the metanephros and the metanephric duct (ureter), which carries excretory products, the Wolffian or mesonephric duct remains as the vas deferens and is used only for the products of the testes.

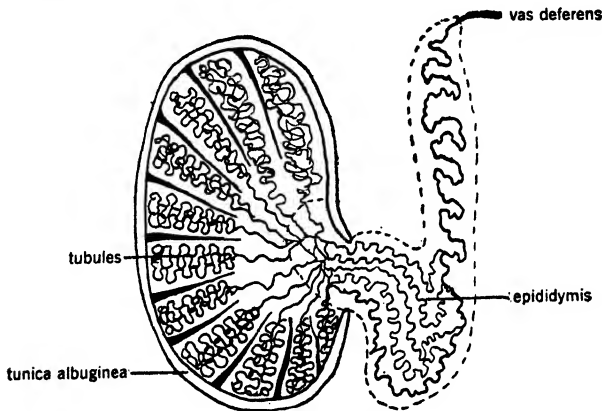


FIG. 291. Diagram of structure of the mammalian testis. After Gegenbaur.

Intromittent Organ

Aquatic forms usually deposit eggs and sperm in water in close proximity, so that the sperm can swim directly to the egg. Amphibians retain the aquatic type of fertilization and have no means for internal fertilization. Some fishes have internal fertilization and develop intromittent organs such as elongated haemal spines. Elasmobranchs may use a modification of the pelvic fin as in *Squalus*.

With land life, beginning in the reptiles, internal fertilization was necessary, and some kind of intromittent organ was developed. The first type of the intromittent organ, found in snakes and lizards, is rather a makeshift structure, that of the snakes being a pair of sacs, the hemipenes which can be everted from the cloacal wall for copulation. The spermatozoa are conducted along grooves, thus reaching the oviducts of the female.

The second type is the penis, which is found in some reptiles, turtles and crocodiles, a few birds, and all mammals (Fig. 289 A, B, C). It is a single structure developed from the ventral wall of the embryonic cloaca. It consists of a ventral part, the corpus cavernosum; two lateral parts, the corpora cavernosa penis; and a distal part, the glans penis. The material of these spongy structures is tough, fibrous connective tissue, with large spaces in which blood can collect, so that the penis is erectile. In the reptiles, the sperm are conducted by an open groove, which closes over in the mammals and becomes continuous with the urethra. In some mammals (carnivores, some primates, etc.) an os priapi or penis bone (Fig. 190) is developed.

Accessory Structures

Accessory structures to the male genital organs appear in many vertebrates. In some elasmobranchs, as in *Squalus*, seminal vesicles and sperm sacs for storage of sperm and for secretory purposes develop in the Wolffian ducts. Cloacal glands are found in some amphibians. With the transition of vertebrates to land life and compulsory internal fertilization, many glands appear along the genital ducts of the male for the function of secreting a fluid vehicle for the sperm. In the higher mammals many glands contribute various secretions, which together with the sperm form the seminal fluid. Prominent accessory glands on the urethra are the prostate and the Cowper's glands. The so-called seminal vesicles at the junction of the vas deferens and the urethra of primates and some other mammals are not storage sacs but vesicular glands. Ampullary glands occur in the terminal part of the ductus deferentes. Urethral glands are located in the wall of the urethra. Other glands not directly associated with the seminal fluid are various skin glands around the prepuce of the penis and around the anus.

Bisexuality

To a certain extent many of the reproductive organs of both sexes are homologous. There is a stage in the development of the individual when most of the reproductive structures are in an intermediate condition. Almost all the reproductive structures of one sex are present in the opposite sex as modified structures or as vestiges. Both the testes and the ovaries arise as the same structure, the sex genes of the individual determining whether the structure will develop as a testis or an ovary. Both the Wolffian and the Müllerian ducts arise in each sex of the higher vertebrates, becoming modified for adult functions according to the sex and the type of kidney. The table shows some of the homologous structures of mammals.

<i>Male</i>	<i>Female</i>
Testes	Ovary
Hydatid (upper part of Müllerian duct)	} Müllerian duct
Uterus masculinus	
Epididymis	Epoöphoron
Paradidymis	Paroöphoron
Wolfian duct	Part of epoöphoron
Urethra (proximal portion)	Urethra
Penis (erectile portion)	Clitoris

Urogenital Systems of Various Vertebrates

Cyclostomes

Excretory Organs

Two types of kidneys are found in the cyclostomes. The adult hagfishes possess a modified pronephric kidney consisting of an anterior and a posterior portion. The posterior portion is considered by some to be mesonephric. The kidney is drained posteriorly by the pronephric duct, which opens on the surface of the body, as no cloaca is present. Adult lampreys possess a mesonephric kidney draining through the pronephric duct.

Reproductive Organs

The gonads are fused into an elongated organ extending the length of the body cavity. Both the sperm and eggs are liberated into the body cavity, and the body cavity of the female is often gorged with eggs. Genital ducts are absent, and both eggs and sperm find their way outside through the genital pores near the opening of the urinary ducts.

Chondrichthyes

Excretory Organs

The adult kidney of the Chondrichthyes is the mesonephros, which has grown backward so that it extends almost the full length of the body cavity. The segmental arrangement, though apparent in its developmental stages, is obliterated in the adult by a multiplication of the tubules. The mesonephros gets its blood supply from the renal arteries, coming off the aorta and from the renal portal system, which sends the blood from the tail and posterior region around the tubules by means of capillaries. The unit of structure of the mesonephros consists of a renal, or Malpighian corpuscle, a convoluted tubule, and a collecting duct, which leads the waste to the mesonephric duct. The peritoneal funnels or nephrostomes may be present, but they are

usually closed off as blind sacs. The mesonephros lies along the back (Figs. 292, 293) close to the body wall, and is separated from the coelom by the pleuroperitoneal lining. By means of the mesonephros, a part of the blood is conducted through this filter at every complete circulation. Since this is a continuous process, the blood is constantly being changed by the removal of its nitrogenous wastes. In the elasmobranch (Fig. 292) the mesonephric or Wolffian duct serves

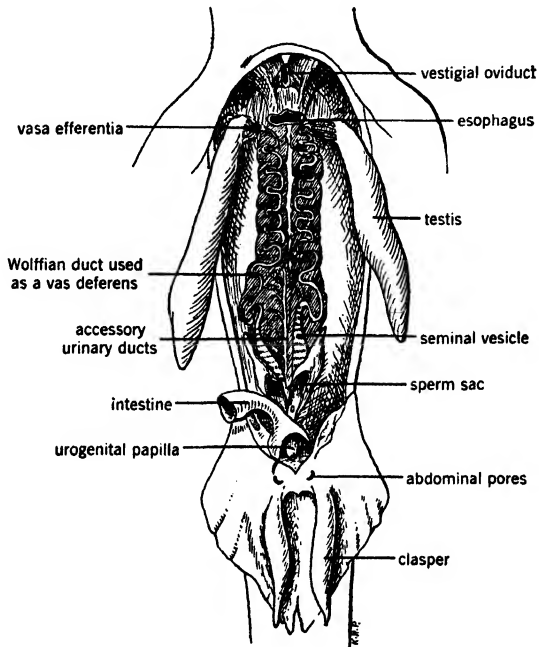


FIG. 292. Urogenital system of a male shark. After Goodrich.

at least partly as a vas deferens and does not drain the posterior part of the kidney. This region is drained by one or more accessory urinary ducts, which empty into the urinary sinus or into the sperm sacs. The uriniferous tubules of the anterior end of the mesonephros are given over to the reproductive system, carry only spermatozoa, and appear to have nothing to do with excretion; the distal (posterior) end carries on the process of excretion and is drained partly or wholly by separate ducts.

In the female elasmobranch, the Wolffian duct (Fig. 293) is only for carrying urine. It extends along the ventral side of the mesonephros and empties into the urinary sinus. As in the male, there is a tendency to form accessory urinary ducts, and there may be several openings of these accessory ducts into the urinary sinus.

Male Reproductive Organs

The testes of the male (Fig. 292) are elongated paired structures that lie against the posterior wall of the body cavity, supported by a mesentery, the mesorchium. The testes are made up of a number of tubules in which the spermatozoa develop. Leading from the testes are small extensions of the uriniferous tubules, the vasa efferentia,

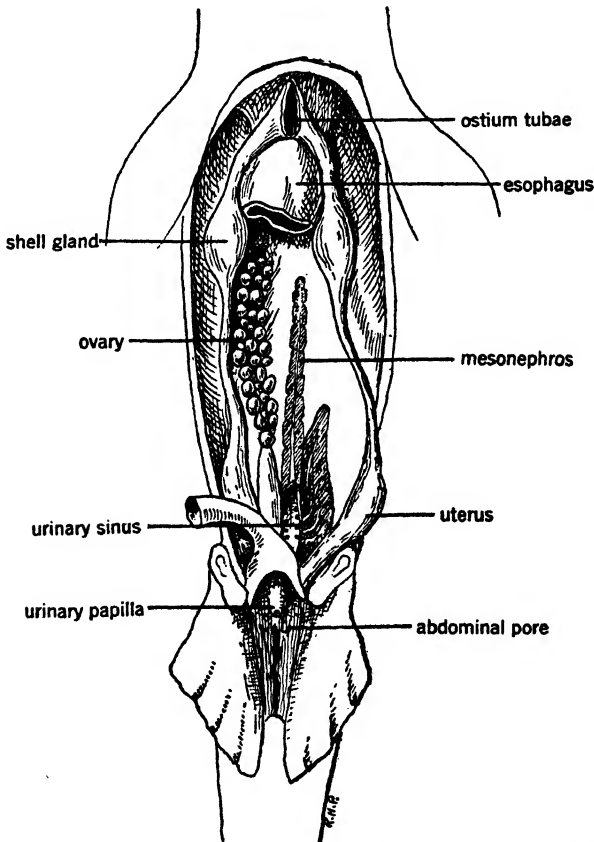


FIG. 293. Urogenital system of a female shark with left ovary removed.
After Goodrich.

which conduct the spermatic fluid through the mesonephros and into the much-convoluted vas deferens or Wolffian duct. The posterior end of the vas deferens is enlarged to form a storage sac, the seminal vesicle, and may have a secondary sac for the extrusion of the spermatic fluid. The spermatozoa are conducted through the urogenital sinus to the cloaca, and in fishes with internal fertilization the pelvic fins may be modified to form an intromittent organ. A vestigial Müllerian duct usually appears anterior to the liver.

Female Reproductive Organs

The ovaries of elasmobranchs are usually long and are attached to the dorsal body wall by a mesentery, the mesovarium (Fig. 293). In contrast to the testes, they are without tubules for the eggs, and the eggs must escape by breaking through the ovarian wall. The ovaries become prominent when the eggs are developing and may fill a large portion of the body cavity in the breeding season. The Müllerian duct, or oviduct (Fig. 293), is a long tube which connects the body cavity with the cloaca. The anterior end of the duct in the falciform ligament forms a funnel-shaped opening, the ostium tubae, derived from a nephrostome, which receives the eggs from the body cavity. The ostia of the two ducts may be fused or may remain separate. The oviduct becomes differentiated into regions: an anterior region in which eggs are fertilized; an area for the addition of the food material; and a shell gland for the deposition of the shell. In fishes that are ovoviviparous the duct becomes modified to form a uterus, in which the eggs develop and hatch.

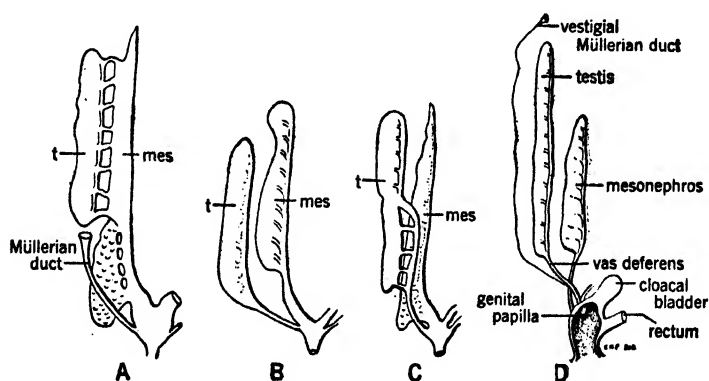


FIG. 294. Urogenital system of male fishes. A, *Acipenser*; B, teleost; C, *Polyperterus*; D, *Protopterus*. After Goodrich.

Osteichthyes

The intermediate fishes, the Chondrostei and Holostei, have urogenital systems (Figs. 294, 295) similar to those of the Chondrichthyes. The teleosts have departed greatly from the regular plan and show many variations in different families. The kidney of most teleosts is a mesonephros draining externally through the former pronephric duct. In many, the pronephroi persist but degenerate into lymphoid tissue. No cloaca is present, and the ducts open with, or adjacent to, the genital ducts. In some marine teleosts, the pronephroi persist and function, although the mesonephroi develop and function posteriorly.

The testes of teleosts are elongated structures suspended by the mesorchium from the dorsal wall (Fig. 294). The ovaries (Fig. 295) occupy a similar position and may be gorged with eggs. Folds of mesentery usually develop and form a tube-like structure holding and carrying both the sperm and the eggs posteriorly to discharge them through genital pores. In some these mesenteric ducts are reduced to mere funnels. No genital ducts which are related to the excretory ducts are developed as in other vertebrates.

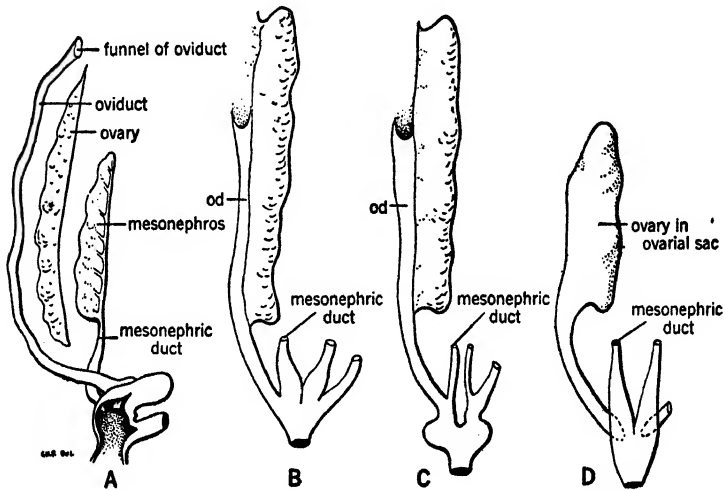


FIG. 295. Urogenital system of female fishes. A, *Protopterus*; B, *Polypterus*; C, *Lepidosiren*; D, teleost. After Goodrich.

In the egg-laying type, which is the more common, the eggs are fertilized externally. The numbers laid may vary from a few to millions; and, of course, the mortality is great. Few fishes show any interest in the eggs after they are laid, letting the young shift for themselves. There are, however, some striking examples of parental protection, where the nest is made and guarded, usually by the male.

Amphibians

Excretory System

The kidney of amphibians is of the mesonephric type, with nephrostomes opening into the body cavity, although those of Anura have become detached from the uriniferous funnels and are fastened to veins. The units of structure, the Malpighian corpuscles, number a hundred or more, in contrast to the very small number in the pronephros. The blood supply comes to the glomeruli direct from the aorta

as in the fishes, and the renal portal is still retained to bring the blood from the tail and posterior end of the body, where it goes through the capillaries that surround the tubules. The kidney is not in the coelomic cavity, but dorsal to it, and is covered by the pleuroperitoneal lining. The mesonephros is an elongate structure, extending from the anterior part of the cavity to the cloaca, to which it is drained by the mesonephric duct. The bladder opens into the ventral side of the cloaca.

Male Reproductive Organs

In the male (Fig. 287), the Müllerian duct, although vestigial and of no functional importance, extends to the anterior end of the coelom. The testes are elongate and yellow, each with an attached adipose body. The vasa efferentia take the spermatozoa through the anterior non-functional part of the kidney, to the mesonephric duct, which carries sperm as well as excretory products. Only the posterior end of the mesonephros is functional. In some amphibians, the spermatozoa are collected and ejected in small, white, cone-shaped packets called spermatophores. These are taken into the cloaca of the female, where the spermatozoa escape and fertilize the eggs. Other amphibians merely liberate the sperm over the eggs as they are laid.

Female Reproductive Organs

The female (Fig. 287) has no immediate connection between the reproductive and the urinary systems. The kidney is the same shape as in the male, but the mesonephric duct carries nothing but the products of the kidneys. Each Müllerian duct, or oviduct, extends to the extreme anterior end of the coelom, where it develops into a funnel-shaped opening, the ostium tubae. Through this funnel, the eggs reach the oviduct, and are carried to the cloacal cavity. (See Fig. 287.)

Adrenals

The adrenals resemble those of the elasmobranchs in that there is a separation into cortical (inter-renal) and medullary (supra-renal) parts. They are small in *Ambystoma* and are located along the inner side of the mesonephros with small bodies along the aorta.

Reptiles

Excretory System

The metanephros (Figs. 296, 297), which is the highest type of kidney, is found in all reptiles, birds, and mammals. Compared to

the lower types of kidneys, it originates more posteriorly in the body cavity, has a different origin, and is slightly different structurally, although the differences are not so much in the kidney itself as in its connections. The pair of kidneys extends along the dorsal wall of the body cavity and is covered by pleuroperitoneal epithelium. Nephrostomes are absent. The renal portal system now tends to go through the kidney structure without passing much blood into this organ. The ureter or metanephric duct, which carries urine to the cloaca, originates as a new structure off the base of the Wolffian duct (Fig. 285), growing posteriorly to the kidney. There is no close connection between the reproductive system of the male and the metanephros, since the old mesonephric duct is now utilized entirely as a part of the vas deferens. Each ureter starts at the anterior end of the kidney and extends posteriorly along the side of the vas deferens, and the pair of them enter the cloaca by a common duct. A bladder is present in some reptiles and develops off the cloaca as a part of the stalk of the embryonic allantoic sac.

Male Reproductive Organs

In the male (Fig. 296), the testes are oval structures, secured to the body wall by a mesentery, the mesorchium. The vas deferens may be much convoluted anteriorly but becomes a straight tube posteriorly. The convoluted portion was originally the mesonephric duct. In crocodiles and turtles a primitive penis lies in the ventral wall of the cloaca. In other reptiles an intromittent organ, the hemipenes, consists of two small folds or sacs, which, when not in use, fit into two small pits just posterior to the cloaca.

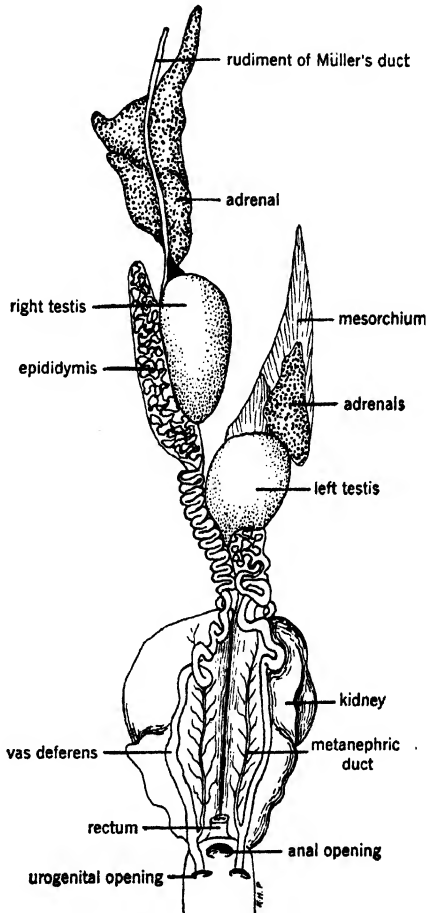


FIG. 296. Male urogenital system of *Sceloporus*.

Female Reproductive System

In females (Fig. 297) the ovaries are about the size of the testes, but they are lobate and show the eggs through the walls, so that they have an entirely different appearance. Each oviduct begins anteriorly

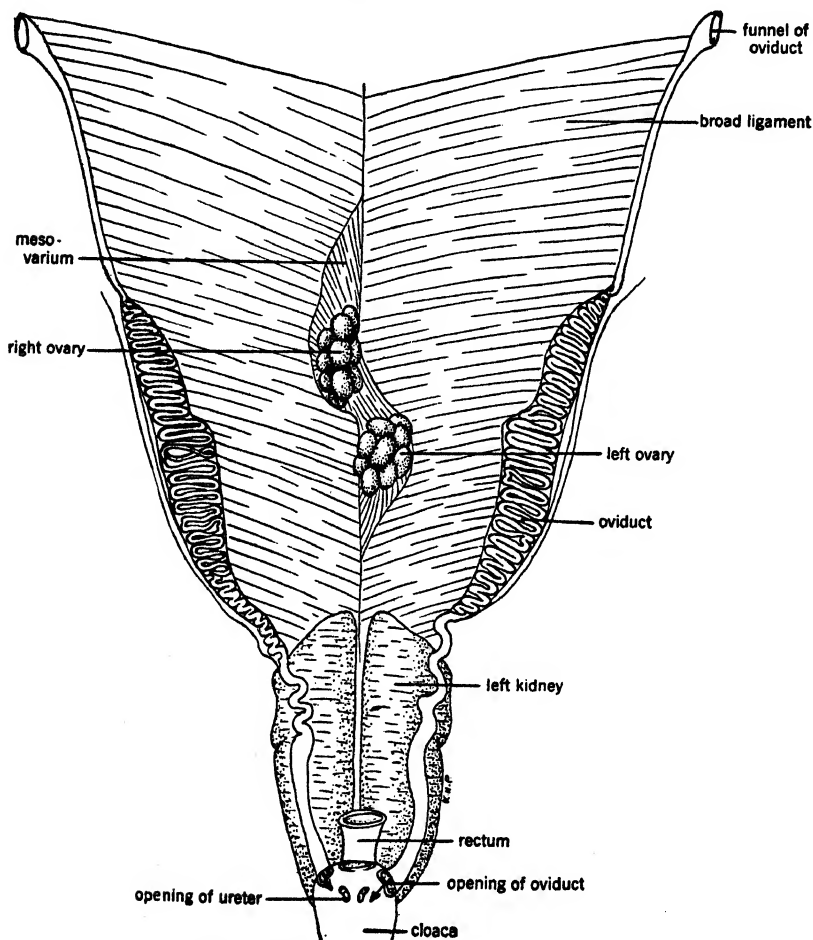


FIG. 297. Female urogenital system of *Scoloporus*.

with a wide funnel-like ostium and extends posteriorly, converging to empty into the cloaca through paired apertures just posterior to the entrance of the ureters.

Birds

Excretory Organs

The metanephric kidneys (Figs. 298, 299) are lobed structures lying close to the synsacrum. The metanephric duct or ureter originates

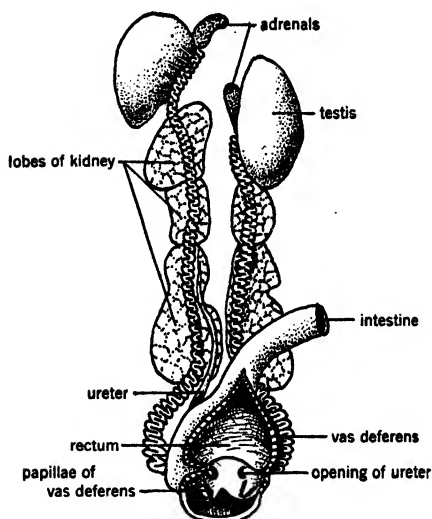


FIG. 298. Male urogenital system of chicken.

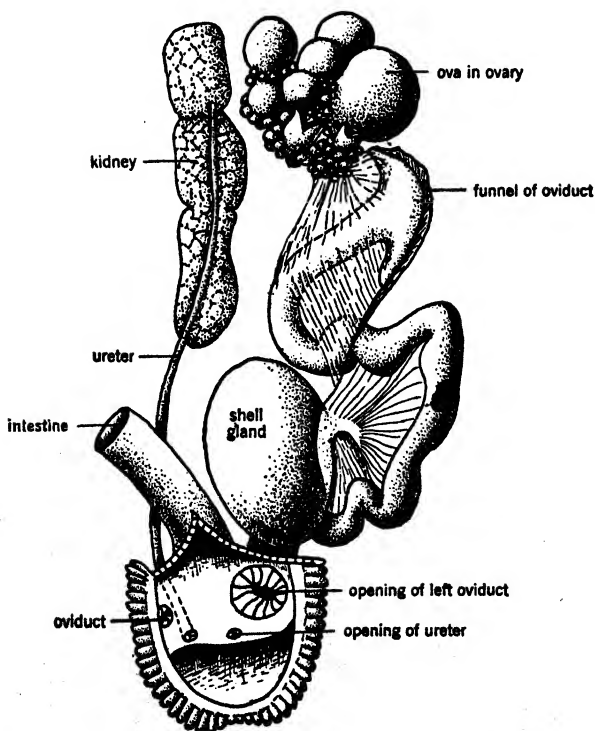


FIG. 299. Female urogenital system of chicken. Redrawn from Schimkewitsch.

on each anterior lobe, extends posteriorly along the ventral side, and enters the dorsal side of the cloaca. The adrenals are attached to the mesial side of the anterior lobes. No bladder is present.

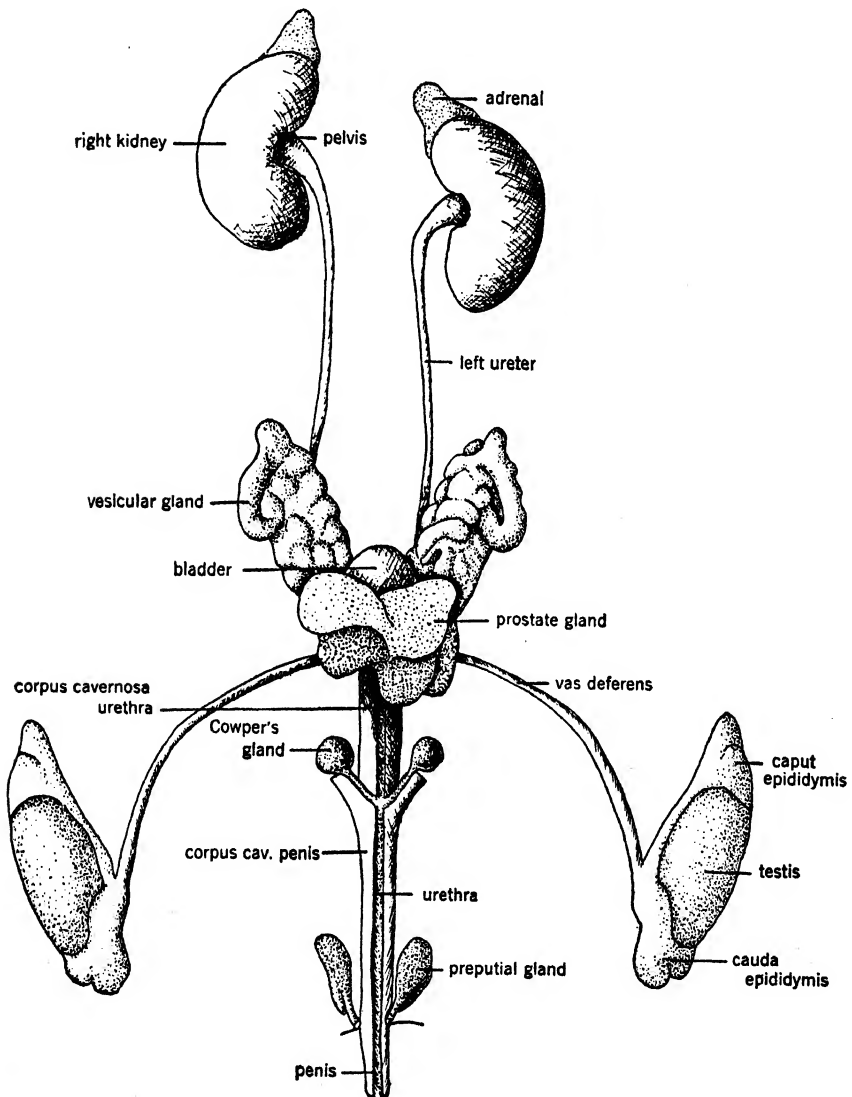


FIG. 300. Urogenital system of male white rat.

Male Reproductive Organs

The testes (Fig. 298), posterior to the lungs and anterior to the kidneys, vary in size according to age. The vas deferens or mesonephric

duct is a convoluted tubule that extends posteriorly along the ventral surface of the kidney, paralleling the ureter for a part of the distance, and enlarging slightly at the distal end to form a small seminal vesicle, which enters the urogenital region of the cloaca by a papilla. The papilla, when enlarged as in the duck and the ostrich, though not in most birds, serves as a penis.

Female Reproductive Organs

Only the left ovary and the left oviduct develop in birds. The single left ovary is posterior to the lungs, and in a mature hen it resembles a bunch of grapes, with eggs in all stages, from small ova to those ripe and ready to be erupted. The oviduct is quite extensive in a laying hen, being about thirty-five centimeters in length, and is divided into four regions. The first region is the funnel, or ostium tubae, which is wide and of ample size; fertilization occurs in the proximal end of this region. The second region is heavy-walled and lined with albuminous glands. The third region adds the membrane, and the fourth supplies the egg with its calcareous shell. A short vagina opens into the cloaca, through which the egg is laid. The right oviduct is short and abortive, remaining only as a vestige, with an opening into the right side of the cloaca.

Mammals

Kidneys

The kidneys (Fig. 300) of the mammal are paired structures on the posterior wall of the coelom, not in the coelomic cavity, but shut off from it by the peritoneal lining. There is a small ductless gland (the adrenal) at the anterior end of each kidney. The right kidney is often slightly anterior to the left. The urine from each kidney is carried by a ureter, from the hilum to the dorsal side of the bladder (Fig. 302). From the bladder the urine passes outside through the urethra, which opens in the male through the penis, and in the female by a separate opening at the ventral border of the vagina.

Male Reproductive Organs

The testes (Fig. 300) are originally in the body cavity as in lower vertebrates, but in many mammals they descend into a scrotum. In very young mammals of this latter type they have their original position and later descend through the inguinal canals to the scrotal sac. Experiments have indicated that testes placed in the body after being in the scrotum do not develop spermatozoa, perhaps because of the high body temperature.

The mammalian testis contains thousands of microscopic spermatogenic tubules, lined with germinal epithelium. This epithelium proliferates the sperm cells (Fig. 291).

The spermatogenic tubules empty into the ductus deferens or epididymal duct (head of the epididymis), which is a much-coiled duct, starting at the anterior end of the testis and running to the posterior end, where it passes forward again to become the vas deferens. The first

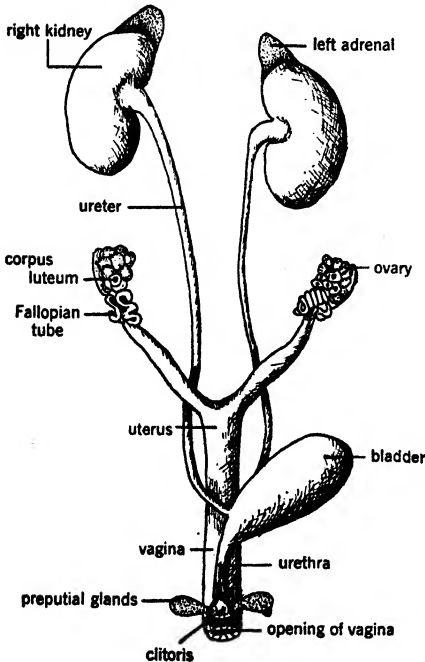


FIG. 301. Urogenital system of female white rat.

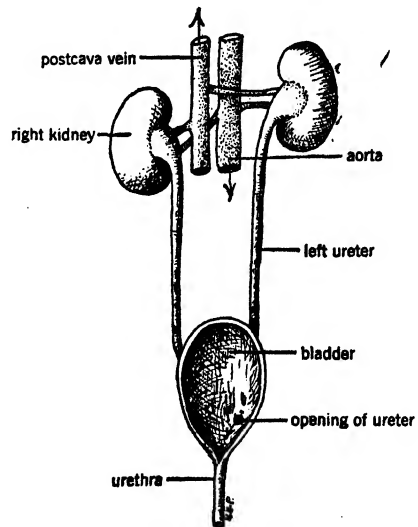


FIG. 302. Diagram of mammalian kidney with its connections.

part or head of the epididymis is homologous with the vasa efferentia of the lower vertebrates derived from the mesonephric tubules. The epididymis forms a cap on each end of the testis, and from it the vas deferens conducts the spermatozoa into the urethra. The penis consists of two lateral corpora cavernosa and a ventral corpus cavernosum, which contains the urethra. These bodies trap the blood in their loose tissues and become erectile. The penis is attached to the symphysis of the ischia. The penis of monotremes retains some reptilian characters, mainly in that only sperm pass through it, the urine passing directly into the cloaca. In marsupials, the penis conducts both sperm and urine, but the glans is divided, a condition correlated with the divided vagina of the marsupial female.

The male has numerous glands of physiological importance that assist in delivering the spermatozoa (Fig. 300). The preputial glands, at the end of the penis, open into the border of the prepuce. The prostate glands, opening into the urethra at the base of the bladder, consist of a pair of lobes at each side and a mass surrounding the proximal end of the urethra. This is a lubricating gland that forms the greater part of the fluid in which the spermatozoa are carried.

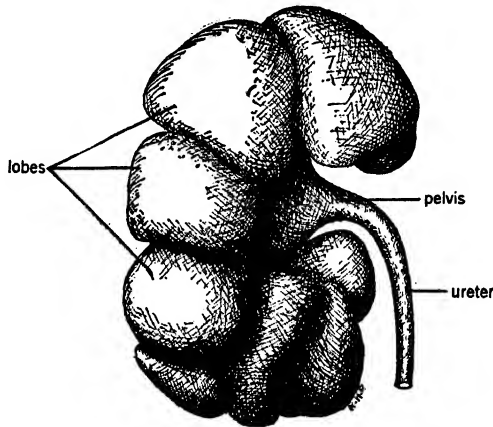


FIG. 303. Lobate kidney of calf.

Anterior to the bladder are two large vesicular glands, which also open into the proximal end of the urethra. On the sides of the vesicular glands are another pair, the ampullary. Cowper's glands add their secretion to the seminal fluid, where the urethra enters the penis.

Female Urogenital Organs

The female reproductive system is not so complicated as that of the male. The kidneys (Fig. 301), have the same relative position as in the male, but the bladder lies ventral to the vagina, the ureters curving around it to reach its base. The oviducts have become modified into a vagina for reception of the male intromittent organ, the uterus for the development of the egg, and the Fallopian tubes which conduct the egg from the ovary to the uterus. The most primitive condition, as in *Ornithorhynchus*, has two oviducts opening separately into the urogenital sinus. In the marsupials, there is some fusion of the bases of the ducts to form a vagina, which may be double or even triple, according to the manner of joining the tubes. All placentals have a single fused vagina, but the uterus, which was originally paired, tends to fuse in higher forms, being two-horned or duplex in rabbits, bipartite

in swine, bicornis in horses, and simplex in the primates and man. (See Fig. 304.)

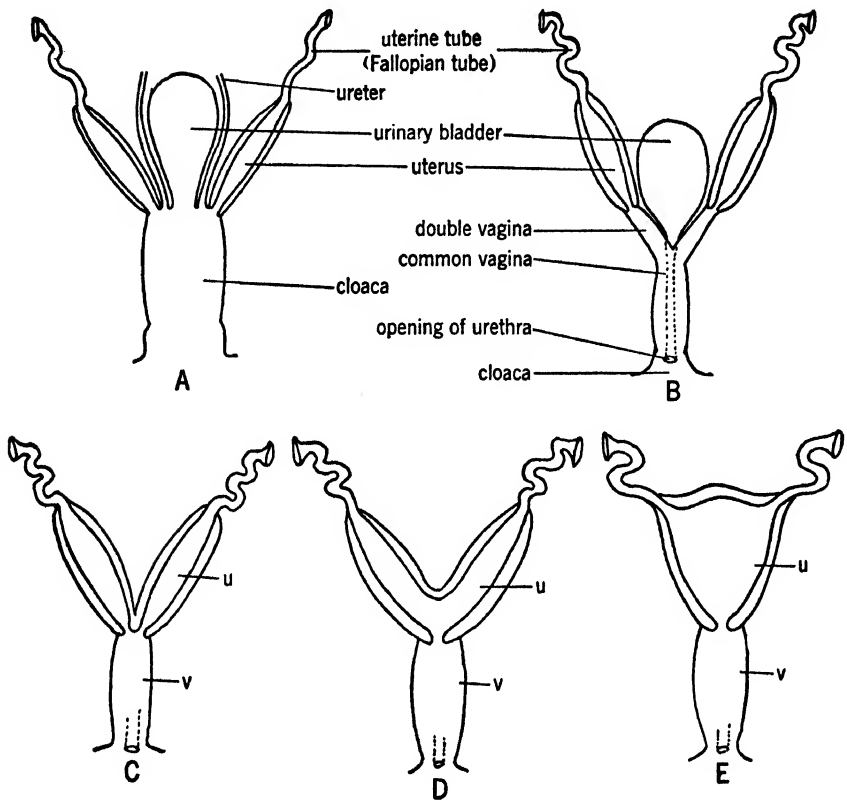


FIG. 304. Oviduct of mammals. *A*, monotreme; *B*, marsupial; *C*, placental with duplex uterus; *D*, placental with bicornis uterus; *E*, placental with simplex uterus.

The uterus opens into the vagina at the cervix, which is a sphincter structure. Above the uterus, the Fallopian tubes lead on each side to the ostia, which open in close proximity to each ovary. In placental mammals the egg is fertilized in the upper end of the Fallopian tube, after it enters through the ostium tubae. It journeys down the tube and attaches itself to the wall of the uterus, where it establishes a connection through the development of a placenta.

CHAPTER FIFTEEN

Nervous System

The nervous system is a highly specialized part of the animal body, simple or complex as the type of the organism demands. It begins to develop at an early stage in the embryo, from the outer germ layer, the ectoderm. From an outside position in primitive forms, the system has retreated inward as the complexity of the animals increased, until in the higher forms the main parts are well buried under bone and muscle and, hence, better protected.

The nervous system is built up by intensifying and adding to the possibilities that already exist in protoplasm, the material from which life is made. First, protoplasm is sensitive, being able to recognize changed or variable conditions; second, it is able to transmit sensations from one part of the mass to another—conductivity; third, it is able to make a response to this stimulation by a correlated action of the parts. By the specialization of these qualities and by adding a large number of parts, the highest nervous manifestations known are possible.

Neurons

The working units of the nervous system are specialized cells, the neurons. Some neurons are modified into neuroglia which act only as supporting cells. Each neuron consists of a cell body, which has a nucleus concerned with nutrition of the cell, and two or more processes, or fibers, which extend out from this body and come in contact with similar processes of other cells, thus connecting the different parts by synapses. The processes are of two kinds: the dendrites, which receive the impulse; and the neurites, or axons, which transmit the impulse to the next connection. The microscopic structure of the cell body shows fine fibrillae which are supposed to conduct the impulses through it. A stimulus, picked up by the dendrites, is transmitted through the cell body to the neurite and passed to the next cell or to other cells. It is assumed that sensations always go through a cell in the same direction. The synapses are "contacts" between the dendrites and axones but involve a space that may be bridged by secretions rather

than with actual contacts. The insulation of the nerve fibers is a covering called the myelin sheath, made up largely of fat and giving the fiber a white appearance. It in turn is surrounded by a cellular layer, the neurilemma. At intervals the myelin layer is pinched in, followed by the neurilemma, which approaches closely to the fibers, forming the nodes of Ranvier.

The fibers from the individual nerve cells are collected to form nerves, and in this way distant parts are connected with the central system and with adjacent structures. Some of these cell fibers are quite long, reaching from the spinal cord to the tips of the limbs, a distance of several feet. The fibers are of two kinds: the sensory fibers, which lead the stimuli in to the central system; and the motor fibers, which take stimuli out to the different parts of the organism. The processes from the neurons grow out from the central system, the brain and spinal cord, and extend to all parts of the animal. Ganglia are formed by the withdrawal of neurons from the central system in the embryological stages.

Reflex Arcs

The most primitive type of the nervous system consists only of effectors, which cause organs or structures to act. This simple system is found only in the lowest invertebrates. The second type results from the addition of specialized receptors, which receive sensations and transmit them in turn to the effectors, thus making a complete arc. With the addition of a third factor, the adjustor, the complexity of the nervous system is greatly increased. This adjustor, deep in the protected regions of the body, makes decisions that are vital to the rest of the organism. In the higher animals an arc somewhat of this type, but probably much more complex, relieves the brain of much unnecessary work by taking care of the minor activities that must be carried on. The nervous system of the invertebrates has been built into nerve cords, each section being related to a division or segment of the body. At first each segment is controlled by its own ganglion, with little correlation between segments; but as complexity increases there is more need for centralization, and a mass of nerve material accumulates in the anterior end, around the mouth and sense organs. When this anterior nerve mass reaches an appreciable size, it begins to take over the functions formerly placed in the segmental nodes of the nerve chains, leaving them little but reflex control.

Divisions of the Nervous System

The central nervous system of vertebrates consists of the brain and spinal cord. The peripheral system consists of the nerves outside of

the central system. The autonomic system is a derivative of the peripheral system. In addition there are specialized sense organs, the ear, nose, eye, taste buds, and a large number of specialized cells sensitive to heat, cold, pain, pressure, etc.

Spinal Cord

The spinal cord of vertebrates is probably the oldest part of the nervous system. Originating as a center of coordination it has become the main connection between the brain and other parts of the body. The cord varies greatly in length with different animals, extending to the tip of the tail in sharks and gradually shortening in the higher forms until it hardly reaches to the sacrum in mammals. It is shortest in teleosts and mammals. In man it barely reaches to the first lumbar vertebra, but the spinal nerves pass on down the neural arch and leave at their respective foramina. The cord is in a protective sheath (neural arch) of cartilage or bone and is surrounded by the same protective coverings as the brain. The cord of tetrapods usually has two enlargements, one in the shoulder region and a second in the pelvic region. Fishes and legless tetrapods such as snakes do not show these enlargements. The cord is always penetrated by the neural canal characteristic of all chordates.

Spinal Cord of Higher Vertebrates

The cord of the higher vertebrates has median, dorsal, and ventral fissures, the depth of which vary in the different classes. In cross-section the cord of mammals is seen to have an inner region of gray matter, consisting of nerve cells and fibers, somewhat in the shape of an H or a butterfly; outside of this is a region of white matter composed of nerve fibers which give it its white color (Fig. 305).

The gray matter (Fig. 306) is made up of nerve cells, fibers, and neuroglia or supporting cells. The pattern of the gray matter varies with the region of the cord. The gray matter is divided into anterior, middle, and posterior columns, the gray matter extending to the periphery of the cord where the fibers come in from the dorsal root, and ventrally where the fibers leave to form the motor roots. The organization of the gray matter is rather complicated, since its functions are so varied. It has reflex connections for impulses that enter the cord and that are sent back to the body for reflex action; it connects the segments of the body by forming collaterals that join two or more segments together; it is the origin of the fibers for the motor roots and receives sensory fibers from the dorsal roots. It is the distributing and sorting structure for both ingoing and incoming fibers, supplies col-

laterals for connecting different levels of the cord, supplies cells concerned in reflex action of the body, and supplies commissures that

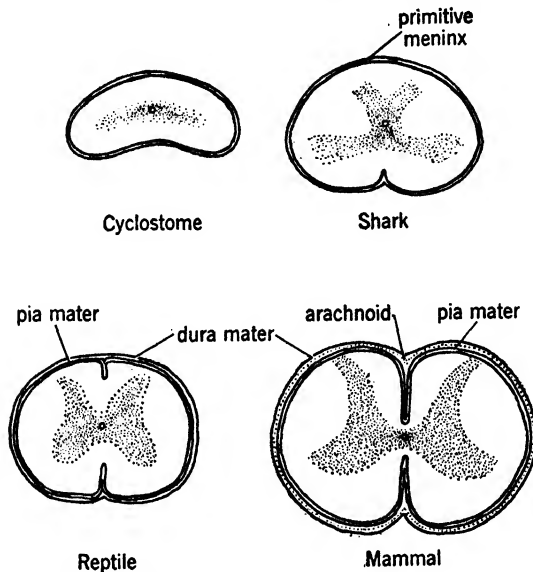


FIG. 305. Diagrams showing structure of spinal cord and meningeal coverings in different vertebrates.

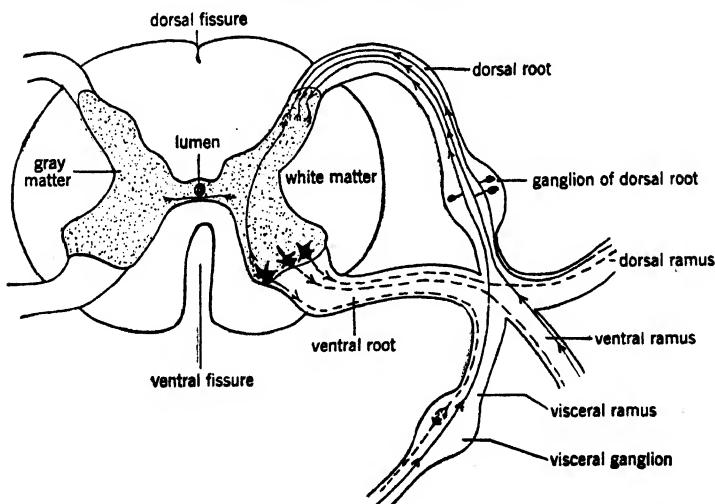


FIG. 306. Diagrammatic section of spinal cord with nerve roots and rami. After Plate.

enable fibers to cross and recross, so that body movements can be synchronized in any way necessary.

The white matter of the cord, consisting of nerve fibers, is divided by

the gray matter into three regions or funiculi: a dorsal, lateral, and ventral. Each region, in turn, has bundles of fibers of varying size and function. The fasciculi, or mixed fibers of different origins and terminations, make up these regions. In general, the fibers of the dorsal funiculus are sensory, those of the lateral funiculus both sensory and motor, and those of the ventral funiculus motor. The sensory or ingoing columns are increasing in size, as they are augmented by additional fibers from the successive spinal nerves; the outgoing or motor tracts become reduced in size for they are sending fibers out to the spinal nerves. The dorsal funiculus contains bundles of fibers going to the different areas of the brain, a large tract to the cerebellum, and others extend on to the anterior part of the brain. The lateral funiculus has both sensory and motor fasciculi, the large rubrospinal taking impulses from the cerebellum and other parts of the brain back down the spinal cord, and the spinothalamic connecting the cord with the thalamus. The ventral funiculus is a motor pathway, and through it, the large pyramidal, thalamic, and other tracts reach the limits of the body.

Spinal Cord of Lower Vertebrates

The spinal cord shows a progressive development through the lower vertebrates. In its most primitive form it seems to be the chief control center, but as the brain becomes more developed the cord tends to assume a more secondary condition. The nerve cord of *Amphioxus* shows no distinct regions of gray and white matter, although the nerve cells are more concentrated in the center. No ventral or dorsal fissures are present.

In cyclostomes the gray matter appears as a broad band (Fig. 305) with the white matter forming definite funiculi. The fishes have the gray matter formed in various arrangements showing distinct columns in shapes ranging from a Y to an H. Dorsal and ventral fissures are often present in fishes but do not become deep until they occur in the land vertebrates, where the columns also tend to become more distinct and assume the characteristic H-shape (Fig. 305).

Coverings of the Cord

In cyclostomes and fishes, the cord is covered with a loose membrane, the primitive meninx (Fig. 305), which is continuous over the brain. In amphibians, reptiles, and birds this membrane seems to have divided into two meningeal coverings, the inner meninx corresponding to the pia mater and the outer tough layer corresponding to the dura mater. In mammals the inner meninx of the reptiles has split forming a delicate pia mater lying next to the cord, and the webby arachnoid tissue

lying just under the dura mater. The dura mater, arachnoid layer, and pia mater are separated by spaces filled with cerebrospinal fluid, allowing the cord to slide easily over the articulating vertebrae.

Spinal Nerves

The spinal nerves are arranged metamerically in pairs. Each spinal nerve of higher vertebrates has a dorsal sensory root with a ganglion and a ventral motor root with no ganglion. These roots are mixed in fishes, containing both sensory and motor fibers. This division of function of the two roots of higher vertebrates was worked out by Bell and is called "Bell's law." Except in cyclostomes, the dorsal and ventral roots unite, and the spinal nerves extend out through spaces between vertebrae. Each nerve immediately divides into three branches: a dorsal ramus to the dorsal body wall, a ventral ramus to the ventral body wall, and a visceral ramus to the viscera and autonomic system. All the rami may contain visceral fibers, but the visceral ramus is made up mainly of this type (Fig. 306).

Brain

In common with the spinal cord, the brain is formed by an invagination of the ectoderm. Phylogenetically, the brain represents an external system removed to the interior of the body. It is a product of cephalization, with the mouth and its sense organs as a focusing point. As in the cord, the ventral part of the brain is essentially motor, and the dorsal part, of later development, is sensory. The dorsal parts represent a superstructure added to the primitive brain as the vertebrates developed. The needs of land life made great differences in the suprasegmental brain. The working structures of the brain consist of many types of neurons in different combinations, small groups called nuclei and large groups or areas of associated neurons, specialized or general in function. A series of ventricles and thin membranes, or choroid plexuses, supply some of the metabolic needs of the brain. Since the brain is a bilateral structure, many cross connections are needed to insure synchronism of action. The larger and better organized cross-fiber tracts are called commissures. Some functions of the brain are localized so that it may be divided into areas that are in control of certain definite parts of the body.

Relative Size of the Brain

There is a rapid increase in the size of brain as the vertebrate scale is ascended and as land life is assumed. The following table (from

Weber after Dubois) shows the ratio of brain weight to body weight for a few of the mammals:

Elephant	<i>Elasphas indicus</i>	1 : 560
Dolphin	<i>Tursiops tursio</i>	1 : 432
Whale	<i>Globicephalus melas</i>	1 : 400
Man	<i>Homo sapiens</i>	1 : 45+
Marmoset monkey	<i>Mystax midas</i>	1 : 26
Spider monkey	<i>Ateles ater</i>	1 : 15

It is interesting to note that the brain of man is neither the largest in actual size nor the largest in proportional weight. Both the whales and the elephants surpass man in the actual size of the brain, and the marmoset and spider monkeys both surpass man in its proportionate size.

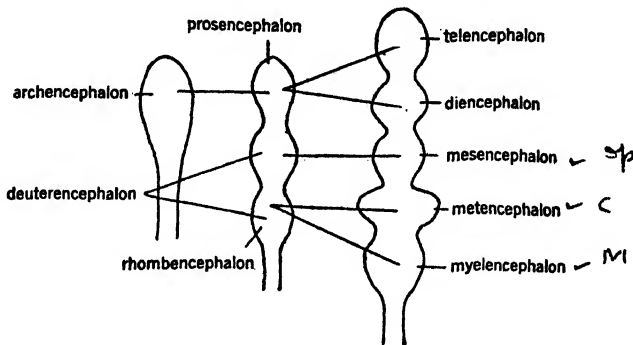
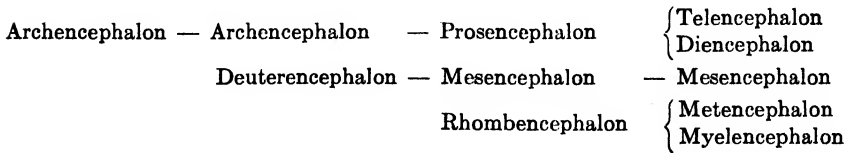


FIG. 307. Diagram showing origin of divisions of brain.

Divisions of the Brain

The divisions of the brain are formed by difference in function and by a difference in the growths of the parts concerned. The lowest type of brain, that of *Amphioxus*, consists of a single vesicle smaller than the cord, which has been called an archencephalon, but its relation to any part of the vertebrate brain may be questioned. Some consider this to be a two-part brain, as it is divided into an anterior region (prosencephalon) lined with ciliated columnar epithelium, and a posterior region (deuterocephalon) marked by a cluster of ciliated cells known as the infundibular organ. The cyclostomes develop the brain first into a prosencephalon and another region, the deuterocephalon, which later divides into two parts, the mesencephalon and rhombencephalon, and in this way the three-part brain is formed. The anterior and posterior parts each divide again, thus forming the five-part brain of the adult cyclostome (Figs. 307, 311). The five-part brain occurs in the adults of all vertebrates. These stages occur in the embryological

development of all vertebrate brains, and it is assumed that the brain has passed through these stages in its evolution. The following diagram outlines the stages in the development of the brain.



Flexures

In the formation of the brain, the more rapid growth of some parts bends the tube so that flexures are made in certain areas (Fig. 308), consisting of an apical or parietal, a nuchal or cervical, and a pontile.

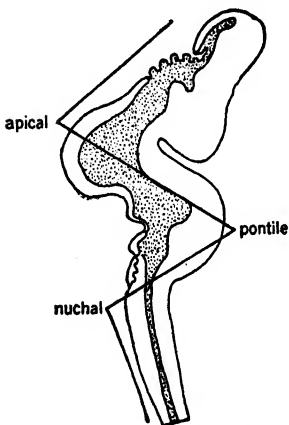


FIG. 308. Brain of snake embryo (*Natrix*) showing flexures.

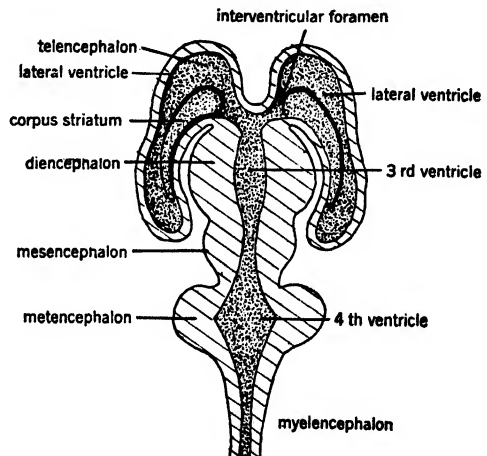


FIG. 309. Brain ventricles. After Villiger.

Although flexures are usually present in the embryo, the flexures are slight in the brains of adult fishes causing the brain to be relatively straight. In birds and mammals, overgrowth of several parts, particularly the cerebrum, causes increasing flexure, so that the brain, although much enlarged, tends to be relatively short and rounded.

Ventricles

The brain, as a continuation of the spinal cord, retains the neural canal, which expands with the growth of the several parts of the brain, forming a series of connected cavities or ventricles. They are filled with cerebrospinal fluid and usually are penetrated by the tela choroidea or choroid plexus, thin membranous sheets filled with capil-

laries. In the telencephalon there are two lateral ventricles, known as the first and second ventricles. They are not well differentiated in the lower fishes since this region is not divided into two complete lobes, but in the higher fishes the division is more complete and the two ventricles are evident. Each opens into the third ventricle in the diencephalon by an interventricular foramen, the foramen of Monro (Figs. 309, 325). The third ventricle is usually narrow, and a large choroid plexus extends down into it and through the interventricular openings into the lateral ventricles. The cavity of the mesencephalon is large in the lower vertebrates and connected with the cavities of the optic lobes, but in the higher animals it becomes a small tube connecting the third and fourth ventricles. The cavity of the metencephalon, the metacoel (Fig. 311), also is found only in the lower forms, for with the growth of the cerebellum it becomes completely obliterated. The fourth ventricle is the cavity of the myelencephalon. It also is covered with a choroid plexus. In higher animals this ventricle extends forward into the metencephalon.

Meninges

The brain has the same coverings as the spinal cord. In the mammals the dura mater is closely attached to the skull, forming a tough, smooth lining. The arachnoid layer is fibrous so that it supplies the insulation from shocks. The inner layer, or pia mater, is closely in contact with the surface of the brain, extending down into the folds, and carrying with it the blood vessels of the surface of the brain for purposes of metabolism. These coverings do not have free spaces between them as they do in the cord, where free movement occurs. The brains of the lower vertebrates have meninges corresponding to those of the cord.

Myelencephalon

The myelencephalon gives rise only to the medulla (Fig. 311), which is very much like the spinal cord in structure but gradually increases in size anteriorly. The cavity of the fourth ventricle, often called the fossa rhomboidalis, is large and has a non-nervous but vascular covering forming a choroid plexus. The nerve paths converge at the sides of the fossa rhomboidalis to get around it and to reach the rest of the central system, thus making a decided swelling at the sides of the fossa. Some of the paths are conspicuous, being marked by evident ridges. The pyramids, a pair of large descending tracts, make large swollen cords on the ventral side of the medulla. On the dorsal side, a number of ridges posterior to the fossa show the ascending gracilis (clava) and the fasciculus cuneatus. Although the medulla

is small in comparison to the rest of the brain, it is not so simple as it appears. The eight nerves of amniotes, starting with the trigeminus, leave the brain from the sides or ventral region of the medulla. Laterally the olive, or olivary nucleus, shows very plainly. The corpus restiforme, or posterior peduncle, forms the connection with the cerebellum. The reflex centers regulating the secretion of saliva, gastric and pancreatic juices, movements of the digestive tube, heart, blood vessels, and organs of respiration are also in this region of the brain.

Metencephalon

The metencephalon consists of two well-differentiated parts: the ventral region, which is a continuation of the brain stem; and the dorsal, or supra-segmental region, the cerebellum (Fig. 311). The ventral part is similar to the same region of the medulla. It contains the nuclei of cranial nerves V and VI in its dorsal wall, and in mammals its ventral side is encircled by the band-like pons (Fig. 324).

The cerebellum varies from a very small and insignificant structure in the cyclostomes to the very prominent lobes of the higher vertebrates. It is an elaborate structure in fishes, where it forms the prominent auricular lobes, but is small in the amphibians (Fig. 316). It gradually increases in size and complexity, reaching its highest development in the mammals. Its origin seems to have been in connection with the vestibular nerve, and it has developed in connection with the increased importance of equilibrium, both in water and in land life. Originally a median structure, it has increased in complexity by the outgrowth of accessory parts, the flocculi (Fig. 321) and paraflocculi of birds and reptiles, and finally the cerebellar lobes of mammals, which completely cover the original parts of the metencephalon. The surface becomes covered with sulci and gyri (Fig. 326) so that its area is very large. On the inside the tracts of fibers from the cortex converge and thus form the arbor vitae (Fig. 325). No nerves take their exit from the cerebellum, but it is rich in connections with other parts of the brain. The large dentate nucleus is the origin of the fibers extending anteriorly into the brain stem. The nucleus fastigii on each side receives axons from the vestibular nerve of the opposite side.

The arrangement of the cells of the cerebellar cortex is much the same for the whole structure, consisting of three layers, an outer, a Purkinje, and an inner layer of nerve cells. The Purkinje cells have large, distinctive bodies, a number of much-branched dendrites, and an axone that connects with the anterior and pontile brachia (Figs. 328, 329).

The connections of the cerebellum with the rest of the brain are through the anterior peduncle (brachium conjunctivum), the posterior

peduncle (restiform body), and the middle peduncle (brachium pontis). The pons of mammals forms a ventral band around the brain stem, connecting the two lobes of the cerebellum (Fig. 324).

The main function of the cerebellum is unconscious motor coordination and the preservation of muscular tonus; the cerebellum has numerous connections with the eyes, ears, muscles, joints, tendons, and other parts of the body. When it is removed the animal is unable to walk but may eventually recover to a limited extent, because other parts of the brain seem able to take over the function of maintaining the equilibrium, especially in mammals.

Mesencephalon

The mesencephalon (Figs. 311, 316, 317, 322, 325) is a short, small region of the brain, connecting much larger parts. Its ventral part is the brain stem, and its dorsal part expands into lobes known as the optic lobes, or corpora bigemina, which do not change much in the different groups, except for the superficial transverse splitting (Figs. 316, 318, 320) to form the corpora quadrigemina (Figs. 325, 327) of the mammals. It is the original eye brain in fishes, but with the growth of the telencephalon its visual function becomes secondary in mammals, which have the main visual centers in the cortex of the cerebral lobes. The ventricle of the mesencephalon originally formed the mesocoels opening into the optic lobes, but in mammals and the higher vertebrates it becomes small and tube-like and is called the iter (Fig. 325). Below the mammals the lobes (corpora bigemina) are usually large and conspicuous, and their importance to sight may be judged by their size. In mammals the posterior lobes of the corpora quadrigemina serve as a relay for auditory impulses. As would be expected, all the nerves connected with the eye muscles come from this division of the brain with the exception of the abducens, nerve VI, whose nucleus is in the metencephalon. The nuclei of nerves III and IV are in the ventral floor of the iter, and nerve II originally had its main connection from this division. The red nucleus, appearing in reptiles, birds, and mammals, is a relay center, which is partially in the diencephalon. It receives fibers coming from the cerebellum through the anterior peduncle and sends them on to the cortex of the telencephalon.

Diencephalon

The diencephalon (Fig. 311) which was formed from the posterior part of the prosencephalon, is a division in which there have been many changes. Its side wall, or thalamus (Fig. 323), is thickened and forms the main part of the brain stem through which most of the connecting tracts must pass to get to the anterior parts of the brain.

The roof, or epithalamus, gives rise to one or two outgrowths or stalks, which terminate dorsally in structures that have been the subject of much speculation. In some of the cyclostomes these structures

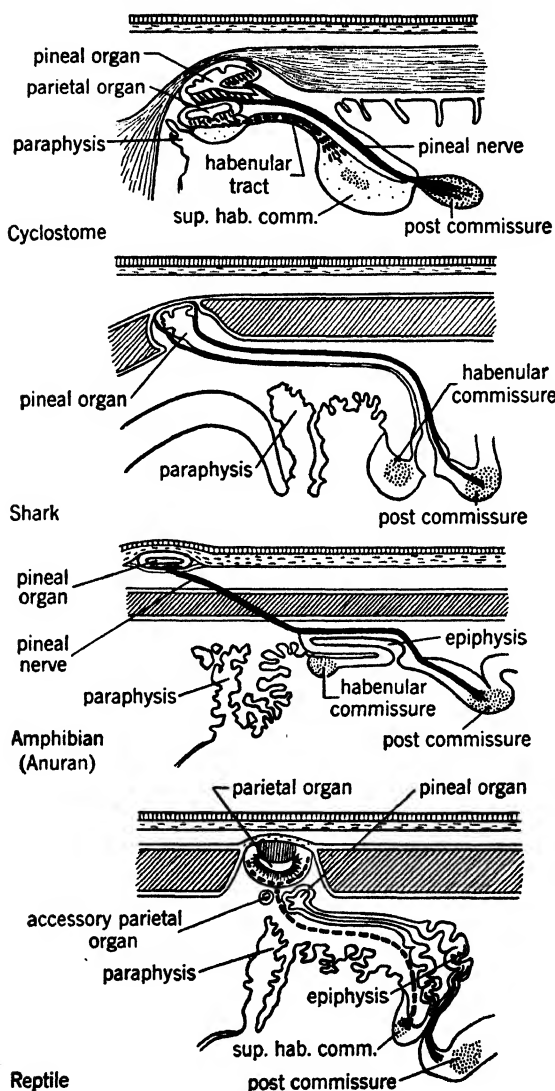


FIG. 310. Diagrams showing the relation of the pineal and parietal organs in vertebrates. After F. K. Studnicka.

arise embryologically as a pair, but in the adult they assume a tandem position. Each of them (Fig. 310) in the cyclostomes bears a vestigial median eye. This is the only instance of the appearance of two median eyes in modern vertebrates. In the vertebrates, above the

cyclostomes, the posterior stalk becomes the epiphysis, bearing the pineal body (apparently an endocrine organ), and the anterior structure bears the parietal body (Figs. 311, 320, 325), which seems originally to have been a median eye in many early vertebrates although it does not function as such in any living form. *Sphenodon*, which has the best-developed vestigial, parietal eye of any living vertebrate, shows a direct retina, a lens, and a nerve. The eye is located in a foramen or socket in the skull between the parietal bones but is covered by scales and does not function.

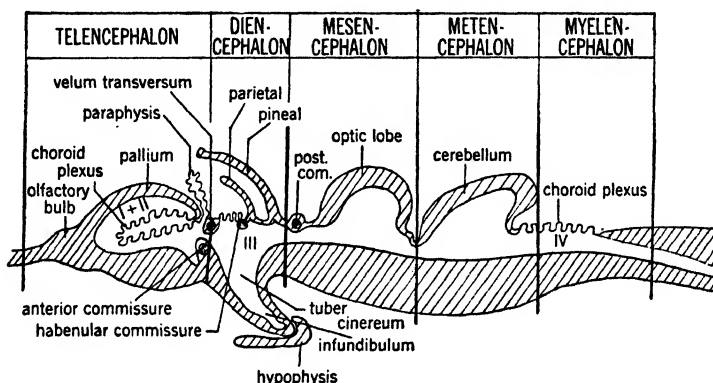


FIG. 311. Sagittal section of brain of shark. After Bütschli.

In many vertebrates, such as fishes, mammals, and some amphibians (Fig. 310), the parietal eye is absent and the pineal structure is present. In many reptiles, however, both structures are present. The difference between the two structures is apparently in their nerve tracts, the parietal fibers going to the left habenular ganglion in the roof of the diencephalon, and the pineal fibers going to the right habenular ganglion. Although open to question, it seems that the left body becomes anterior, forming the parietal eye, and the right body assumes a posterior position, forming a pineal body. In birds and mammals, the pineal body, covered by the other parts of the brain, functions as a gland of internal secretion. Anterior to these epiphyseal structures, the roof is covered by a vascular choroid plexus. The pulvinar nucleus (Fig. 323) is a relay connecting the eye, the lateral geniculate, and the visual cortex of the telencephalon. In mammals the medial geniculate is connected with the inferior cerebral commissure, and the lateral geniculate is a relay between the eye and the cerebral cortex.

The tuber cinereum (Figs. 322, 325) is a ventral extension of the floor of the diencephalon (hypothalamus), terminating in a tube, the infundibulum. This in turn is connected with the hypophysis (Fig. 325), a diverticulum formed embryologically from the mouth (Rathke's

pocket), which eventually closes again, leaving this tissue on the ventral side of the infundibulum. In the sharks, the infundibulum becomes enlarged and folded to form the dark-colored saccus vasculosus. The hypophysis, an endocrine gland that appears in all vertebrates, fits into a small depression in the floor of the brain case, the sella turcica.

Two mammillary bodies (Fig. 325), in man about the size of peas, lie just posterior to the hypophysis and are concerned with the sense of smell. Anterior to the hypophysis, the chiasma (Fig. 324) of the optic nerves is a striking landmark. In the higher mammals, the optic nerves send most of their fibers through the lateral geniculates to the visual areas of the cerebral lobes. No nerve nuclei are found in the diencephalon.

The cavity of the diencephalon is the third ventricle (Figs. 311, 325), a very narrow, slit-like space, encroached upon by the growth of the walls or thalamic region. The soft commissure (Fig. 325) joins the walls in the higher animals, forming a bar-like connection across the ventricle. The third ventricle opens into the lateral ventricles by a pair of slit-like openings, the interventricular foramina (the foramina of Monro) (Fig. 325). The choroid plexus, extending down from the roof, pushes forward so that a branch enters each lateral ventricle. The commissures are the superior (habenular) and the massa intermedia (commissura mollis, soft commissure).

Telencephalon

The anterior region of the original prosencephalon becomes the telencephalon and is the most variable of all the divisions of the brain (Fig. 311). In fishes and lower vertebrates it is made up largely of partially divided lobes, which are sometimes referred to as cerebral hemispheres, although they are hardly comparable to those of the higher vertebrates as most of this part of the brain is devoted to the sense of smell. In land vertebrates, the cerebral part, containing the centers of volition and control, increase in size until in man these parts cover the rest of the brain, the olfactory centers occupying only a minor portion. The roof of the telencephalon is the pallium, and the floor is the corpus striatum. In sharks (Fig. 311) the pallium is swollen, but in the teleosts (Fig. 312) it is thin. In land vertebrates great changes occur in the pallium, which thickens and develops into two distinct dorsal cerebral hemispheres with their millions of neurons, and in the higher forms the surface area is increased by convolutions (sulci and gyri). The concentration of neurons into a cortex or layer near the surface first appears in reptiles and birds but becomes best developed in mammals, where it forms a definite but thin layer covering the cerebrum.

With the development of the cerebrum, other parts of the brain are enlarged or changed. The cerebrum establishes better connections with these parts. In fishes there is little connection between the telencephalon and other parts of the brain, although there are some fiber tracts that extend to the basal region. Starting with the tetrapods, there is an increasing number of tracts connecting the telencephalon with the posterior regions of the brain and spinal cord; and in mammals, practically every part of the central nervous system has either direct or indirect connection, through relays with the cerebral hemispheres.

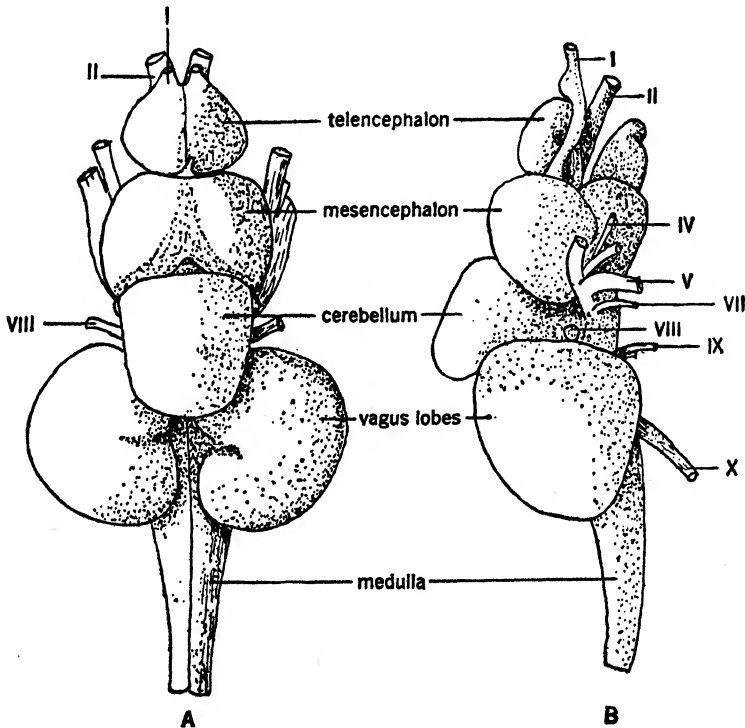


FIG. 312. Brain of teleost (*Ictiobus*) after Herrick. A, dorsal; B, lateral.

✓In fishes the front of the telencephalon is pushed out into a pair of olfactory bulbs which receive the olfactory nerves from the nasal sacs. The olfactory bulbs are connected to the cerebral (olfactory) lobes by a pair of tracts, each of which has connections to the lateral walls of the diencephalon, but in higher vertebrates, with the development of the pallium, the olfactory portion is shifted to the ventral side and becomes a very small part of the telencephalon. The basal region, the corpus striatum, assumes new importance and grows along with the pallium, assisting in making the required new connections

with the other parts of the brain. It becomes enlarged and differentiated, and its neurons become localized for motor control. A new pathway leads from the walls of the diencephalon to the ventral region of the corpus striatum and thence to the cortex of the cerebral lobes. The fibers in this pathway pass through the thalamus and then through the caudate and lentiform nuclei.

In the higher vertebrates the cross connections, or commissures, are increased with the development of the cortex. In addition to the original anterior commissure, which is in the lamina terminalis of the fishes, two extra commissures are formed: the pallial commissure, which splits to form the large corpus callosum (Figs. 323, 325), found in mammals above the monotremes; and the hippocampal commissure, which connects the hippocampal regions of the telencephalon and forms the pillars of the fornix. The corpus callosum serves the dorsal areas of the cortex.

The pathway from the spinal cord to the cortex is through the thalamus of the diencephalon, then through the internal capsule, and out to the cortex through the corona radiata. This contains both the afferent and efferent fibers. It is not developed to any extent in the lower forms but reaches its maximum development in the mammals. Through this new system all parts of the brain as well as all parts of the body are connected with the cortex. The cortex itself is made up of a thin layer of cells, a few millimeters thick, which entirely covers the cerebral lobes. The rest of the material of the lobes consists of the connecting fibers.

In the lower forms the surface of the telencephalon is smooth, but as the higher forms are approached there is a tendency for the formation of lobate structures through the unequal growth of some parts of the surface. In man each cerebral lobe may be subdivided into five lobes: the frontal, parietal, occipital, and temporal lobes, and a covered insula of Reil, which lies under the temporal lobe. These are marked off by fissures to form fairly natural divisions. There is a localization of function in parts of the cortex, relatively small areas being in control of definite functions, such as hearing, seeing, smelling, word perception, writing, and movements of parts of the body.

Cranial Nerves

The cranial nerves, connected with the brain itself, are variable in number: eight pairs in the cyclostomes; ten in the fishes and Amphibia; and twelve in the reptiles, birds, and mammals. The additional nerves of the brain series seem to have come from the inclusion of more of the spinal nerves within the brain case.

The problems presented by the cranial nerves are: first, what they

represent; and, second, how they can be compared with spinal nerves. In protochordates and cyclostomes, nerves come off from the central system both dorsally and ventrally, those from the dorsal region with ganglia and those from the ventral side without, but the two do not unite as do the true spinal nerves of the higher vertebrates. It is assumed that the cranial nerves were of the same form originally, that the motor nerves are those that were ventral and unganglionated, and that the sensory nerves, with their ganglia, are comparable to dorsal spinal nerves. This gives rise to the theory that the cranial nerves that are mixed once had a double origin. No cranial nerves have the typical form of spinal nerves.

The problem of the cranial nerves with the original head segmentation is still unsolved, since conclusions are still indefinite as to just what is represented in the head region. A study of the developing head and brain seems to indicate that from nine to thirteen segments are concerned in its formation, and with these the cranial nerves are associated.

Cranial nerves I, II, VIII and probably the nervus terminalis are made up of sensory fibers only. Nerves IV and VI are purely motor. The rest, with the possible exception of nerve III, have mixed fibers. The only nerves leaving the head region and extending to the body are X and XI. Nerves IX, X, and XI form a group that belonged to the gill region in fishes and appear to be composite nerves in higher forms. (See table on cranial nerves, p. 399.)

Terminal Nerve

This is a small nerve which was not included in the original numbering system because it was not discovered until long after the system had been established. Pinkus discovered it in the fish *Protopterus*, in 1895, and it has since been found to be practically constant throughout the vertebrates, although only embryonic in the higher vertebrates. It originates in the membrane of the nose and is connected with the telencephalon. It is not well understood and has been assumed to be sensory, although it may belong to the autonomic system. It is possible that it is a part of the olfactory tract and not an independent nerve. In the shark it appears as a tiny nerve leaving the nasal sac and running parallel to the olfactory tract to enter the telencephalon.

Olfactory Nerve, I

The olfactory nerve originates in the olfactory region of the nose and supplies the innervation of the sense of smell. It really is divided into a number of small branches which enter the olfactory bulb of the telencephalon. The extension to the brain is the olfactory tract and hence part of the brain since the neurons extend the length of

the structure, and the olfactory nerves themselves are merely the small twigs that extend between the end of this tract and the mucous membrane of the nose or nasal pits.

Optic Nerve, II

The optic nerve, also a tract, originates in the retina, where it receives the impulses from the rods and cones. It enters the brain on the ventral side of the diencephalon, just anterior to the hypophysis, and connects with the optic centers of the mesencephalon. In lower forms the connection with the mesencephalon is constant, but in higher forms there is a gradual modification, with more and more of the fibers leading to the optic centers of the cerebral cortex. At its entrance to the brain, a chiasma is formed in which the fibers merely cross in the fishes but intermingle in many of the higher forms, so that the fibers from each eye are directed to both sides of the brain, thus giving binocular vision.

Oculomotor Nerve, III

This nerve which originates in the mesencephalon and takes its exit from the same structure, is a motor nerve and innervates the eye muscles, namely, the superior, inferior, and internal recti, the inferior oblique, and the ciliary muscle and process. It acts as a part of the parasympathetic system in the ciliary process. (See Fig. 324.)

Trochlear Nerve, IV

This is a motor nerve originating in the mesencephalon, taking its exit from the dorsal side, and innervates the superior oblique muscle. (See Figs. 316, 319.)

Trigeminal Nerve, V

The trigeminal nerve originates in the brain from two nuclei that extend from the mesencephalon through to the medulla. One nucleus is sensory and the other motor, making it evident that it has two roots and is a mixed nerve. Its branches are sensory except the mandibular branch which has some motor fibers. The trigeminal was originally the nerve of the first gill arch and hence of the upper and lower jaws. It leaves the brain from the side of the medulla in close connection with the exits of nerves VII and VIII. It has three branches in higher vertebrates. In fishes it is divided into four branches. The first two divisions, the superficial ophthalmic to the region of the orbit and the deep ophthalmic to the region of the nose, are not divided in other vertebrates. The deep ophthalmic has its own ganglion and probably represents a separate nerve. It was originally not a part of the tri-

geminal and is independent in the selachians and cyclostomes. It really constitutes the sensory part of the same head segment for which the oculomotor is the motor element. The trigeminal represents the sensory part for another head segment, whereas the trochlear represents the motor element.

The maxillary branch, coming from the Gasserian ganglion, innervates the maxilla and its teeth. The mandibular branch, which extends ventrally, innervates the mandible and its teeth and most of the muscles of mastication. It has several subdivisions, one of which serves the tongue and is called the lingual nerve in mammals. (See Fig. 324.)

Abducens Nerve, VI

This nerve has its origin in the anterior part of the myelencephalon and leaves the brain from the ventral side of this structure, innervating the external rectus muscle. This is the last of the eye-muscle nerves. (See Fig. 324.)

Facial Nerve, VII

The facial nerve originates in the medulla and leaves the brain from the side. It was originally the nerve of the second hyoid arch. It serves the region in which there has been much shifting of parts and decided changes in function, so that there is a considerable difference between the fish and the tetrapod condition. In the lower animals this ganglionated nerve parallels the region innervated by nerve V but is concerned principally with the lateral-line structures, such as the ampullae of Lorenzini and the series of lateral-line canals on the heads of fishes and amphibians. In fishes there are branches innervating the different sensory canals of the head region, the membranes of the mouth, and some of the muscles of the hyoid arch. In the higher tetrapods, the elimination of the sensory canals causes the dorsal branches to disappear, but three branches are retained, the palatine, internal mandibular, and a part of the hyomandibular. The internal mandibular, or chorda tympani, takes a peculiar course through the middle ear before going to the tongue. Fibers from the chorda tympani form a part of the parasympathetic system in control of the salivary glands. In mammals the chief function of the facial nerve is to control the mimetic musculature. (Fig. 324.) This nerve is considered as mixed but, aside from the lateral line components, is largely motor.

Auditory Nerve, VIII

This nerve, conducting sensations from the ear, enters the brain close to *facialis* and is probably also a part of the original acoustico-lateral line system. Nerves V, VII, IX, and X are involved in the

lateral-line system of aquatic vertebrates. As the sensory cells of the lateral-line organs are similar to those of the inner ear, there seems to be a relation between this system and the acoustic system; hence they are termed the acoustico-lateralis system. The roots of the first four nerves of the lateral-line system enter the same region of the medulla as the auditory nerve. In the lower vertebrates the auditory nerve connects with a single nucleus in the brain, but in the land vertebrates, with the development of the organ of Corti, there is a division of the nerve into two branches, each having its own nucleus in the brain, one for the fibers from the semicircular ducts and the other for the cochlea. (See Figs. 324, 353 B.)

Glossopharyngeal Nerve, IX

This is the segmental nerve of the third branchial arch and originally had a pre- and a post-trematic branch. It originates in the medulla; leaving the side of this structure, it forks around the second gill cleft, innervates the muscles of the third branchial arch in fishes, and sends a branch to the palate, which joins the palatine branch of the facial nerve. In mammals it innervates the pharyngeal region and a part of the tongue. It has the petrosal ganglion at its base. It is mixed in character. (Fig. 324.)

Vagus (Pneumogastric), X

Originally the pneumogastric, or vagus, was a part of the lateral-line system. It represents several joined nerves similar to the ninth. It leaves the side of the medulla by several roots, each originally having its own ganglion but later formed into a single mass. In fishes it supplies the remaining gill arches with pre- and post-trematic branches and with a long lateral branch that extends posteriorly to supply the lateral-line organs. With the loss of the gills, it still continues to supply the gill muscles retained in the throat of the tetrapods. With the dropping out of the lateral line, the pneumogastric becomes a nerve of the viscera, sending branches to the digestive, respiratory, and circulatory systems. The heart, lungs, and stomach are well forward in the lower forms so that they are within the region controlled by the original vagus nerve, and as these structures have retreated posteriorly in the body cavity in tetrapods the nerve has followed them. It is also connected with the autonomic system as a part of the parasympathetic control. (See Fig. 324.) It is mixed.

Spinal Accessory Nerve, XI

This nerve is found only in reptiles, birds, and mammals. It seems to be formed from a part of the vagus that has become independent

CRANIAL NERVES

No.	Name	Brain roots	Type	Distribution or origin
0	Nervus terminalis	Telencephalon	Sensory	The mucous membrane of the nasal capsule
I	Olfactory	Telencephalon	Sensory	The mucous membrane of the nasal capsule
II	Optic	Mesencephalon	Sensory Brain tract	The receptors of the retina of the eye
III	Oculomotor	Mesencephalon	Motor	ciliary process superior rectus internal rectus inferior rectus inferior oblique
IV	Trochlearis	Mesencephalon	Motor	superior oblique
V	Trigeminalis	Myelencephalon	Mixed	ophthalmicus superficialis: skin of head ophthalmicus profundus: skin of snout and lateral line maxillary branch: ventral surface of snout, mouth cavity, region of the upper jaw mandibular branch: skin of ventral side of head, jaw muscles
VI	Abducens	Myelencephalon	Motor	lateral rectus
VII	Facialis	Myelencephalon	Mixed	ophthalmicus superficialis: suborbital canals, ampullae of Lorenzini, lateral-line canals palatine: dorsal region of mouth buccal: ampullae of Lorenzini, lateral-line organs, mouth region hyomandibular: lateral line mandibular: lower jaw
VIII	Auditory	Auditory centers of metencephalon	Sensory	sensory structures of ear
IX	Glossopharyngeal	Myelencephalon	Mixed	third gill mouth hyoid region
X	Vagus (Pneumogastric)	Myelencephalon	Mixed	all gills posterior to third lateral-line organs ramus intestinalis to organs of circulation and digestion
XI	Spinal accessory	Myelencephalon	Motor	Trapezius and sterno-cleido-mastoid muscles, with vagus to organs of circulation and digestion
XII	Hypoglossal	Myelencephalon	Motor	Muscles of pharynx and larynx, tongue muscles

in amniotes and, with the incorporation of cervical vertebrae with the skull, has combined with cervical spinal elements. The nucleus is in the medulla, and its exit is from the same structure. In fishes, it is a spinal nerve and innervates the muscles of the segment posterior to the skull; in mammals, it innervates the trapezius and sterno-cleido-mastoid muscles. (See Fig. 324.) It is purely motor.

Hypoglossal Nerve, XII

The hypoglossal has its nucleus in the medulla and takes its exit from the side of the structure. It innervates the tongue muscles which were originally hypobranchial muscles from the posterior region of the branchial arches. In fishes this nerve is a spinal nerve as the hypobranchial muscles still function as gill muscles. In tetrapods, with the movement of these muscles into the tongue, this nerve moved into the brain case. (See Fig. 324.) It is present as a cranial nerve only in reptiles, birds, and mammals. It is purely sensory.

Peripheral Nerves

The peripheral system, together with its auxiliary, the autonomic system, furnishes the means of nerve distribution. The outlets from the spinal cord (Fig. 306) are through the metameric spinal nerves that send fibers to all the regions of the body. The origin of each fiber is in the ganglia which early in the embryo sends out fibers that are to form all the future connections with the body. On the dorsolateral walls of the spinal cord, crests are developed into which the neurons migrate to form the sensory ganglia of the dorsal roots. Ventrally on the cord other fibers extend out, forming the ventral roots, but these are without ganglia, since their neurons are within the cord itself. The dorsal and ventral roots of each nerve join together and immediately subdivide into three branches, the dorsal, ventral, and visceral rami. From these branches fibers grow to all parts of the body. The fibers may be divided into four types: somatic sensory, visceral sensory, somatic motor, and visceral motor. The origins of the sensory fibers are in sense receptors in all parts of the body. The motor fibers in a similar manner must eventually reach the different regions where they end in muscles and other structures. The autonomic system, containing both sensory and motor fibers, which grow from the visceral rami, controls the viscera. In regions of the body where there is much activity, nerves from a number of sources become interlaced and closely connected by collector nerves, thus forming subsidiary control centers called plexuses.

Four prominent plexuses are associated with the spinal nerves in the higher vertebrates. These are the cervical, brachial, lumbar, and

sacral plexuses which often combine to form the cervicobrachial and the lumbosacral plexuses. Only the ventral roots take part in these plexuses. A branchial plexus innervates the hypobranchial muscles of fishes and cyclostomes and becomes the cervical plexus of the tetrapods. The hypobranchial nerve, originating from the branchial plexus, becomes the hypoglossal nerve of amniotes.

Plexuses vary in the pattern of their lacework and even in the number of nerves involved within individuals of the same species. Man ordinarily has the first four spinal nerves in the cervical plexus. The last four cervical and the first thoracic nerves form the brachial plexus. The first four lumbar nerves enter the lumbar plexus, and the fifth lumbar and the five sacral nerves are in the sacral plexus. The phrenic nerve of mammals, which innervates the diaphragm, originates from the spinal nerves of the cervical plexus, indicating that the diaphragm had a cervical origin. Numerous plexuses occur in the viscera especially in connection with the autonomic system.

Autonomic System

The autonomic system consists of a part of the peripheral nerves that have been somewhat isolated from the rest to form a subsystem for special work. It is formed mainly from neurons that have withdrawn from the ventral part of the spinal cord, and consists of ganglia and nerves with an organization similar to that of the main system, since it has receptors, adjustors, and effectors, but is not under conscious control. These nerves and ganglia of the autonomic system complete the machinery necessary to control such organs as the heart and lungs, which have a continual action; and the digestive system, in which non-striated muscles continue to work for a long period of time. All the movements initiated by this system are rather slow in contrast to the fast action possible in the voluntary system.

The autonomic system is known only in the vertebrates, but it seems probable that their invertebrate ancestors used a part of their nervous system for a similar purpose. Systems resembling the autonomic system have been recognized in the arthropods, but they are not homologous with the autonomic system of vertebrates. It is possible that some part of the invertebrate system has supplied the basis for its development. However, these conjectures are highly questionable and do not answer the question of the origin of the autonomic system of vertebrates.

Little is known about the autonomic system of the lower vertebrates. Starting with the cyclostomes and fishes, there is a progressive development of the system that is much better known in the higher forms of vertebrates. In cyclostomes, sympathetic fibers are associated with

the vagus and spinal nerves. The autonomic system of sharks shows no division into sympathetic and parasympathetic parts. The system consists of paired segmental ganglia along the mid-dorsal wall, imbedded in the wall of the postcardinal sinuses and posteriorly in the kidneys. Plexuses, which form in the viscera, connect the ganglia, but no trunks are present. Sympathetic ganglia are also distributed

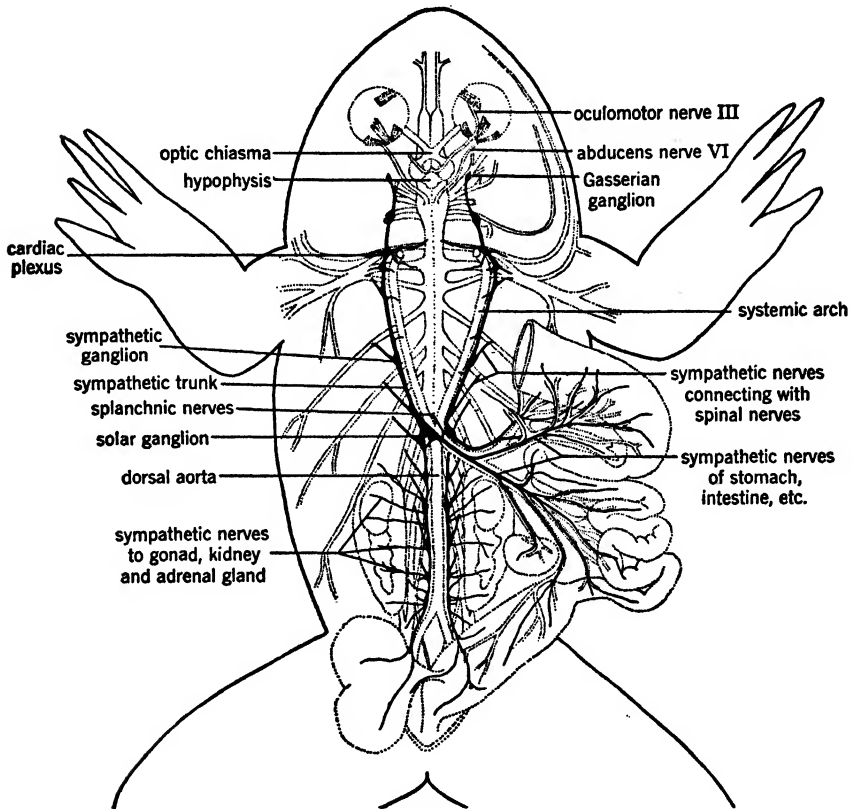


FIG. 313. Bullfrog (*Rana catesbeiana*). Nervous system (ventral view); sympathetic nervous system shown in solid black. From Wodsdalek.

among the gills. In amphibians (Fig. 313), the paired segmental ganglia are connected by a pair of sympathetic trunk nerves, and this sets the pattern for the tetrapod autonomic system.

The system in the higher vertebrates (Fig. 314) is often divided for convenience into the parasympathetic and sympathetic systems, the parasympathetic consisting of the fibers carried by cranial nerves III, VII, IX, and X and sacral nerves 2, 3, and 4. The oculomotor sends fibers to supply the ciliary muscles of the eye, the facial nerve sends fibers to the salivary and submaxillary glands; the glossopharyn-

geal to the otic ganglion; and the vagus to the viscera, including the heart, lungs, vasomotor system, bronchi, stomach, intestines, liver, pancreas, and kidney. The posterior part of the autonomic system connected with sacral nerves sends fibers to the colon, bladder, and urogenital organs. Fibers coming through these nerves are usually

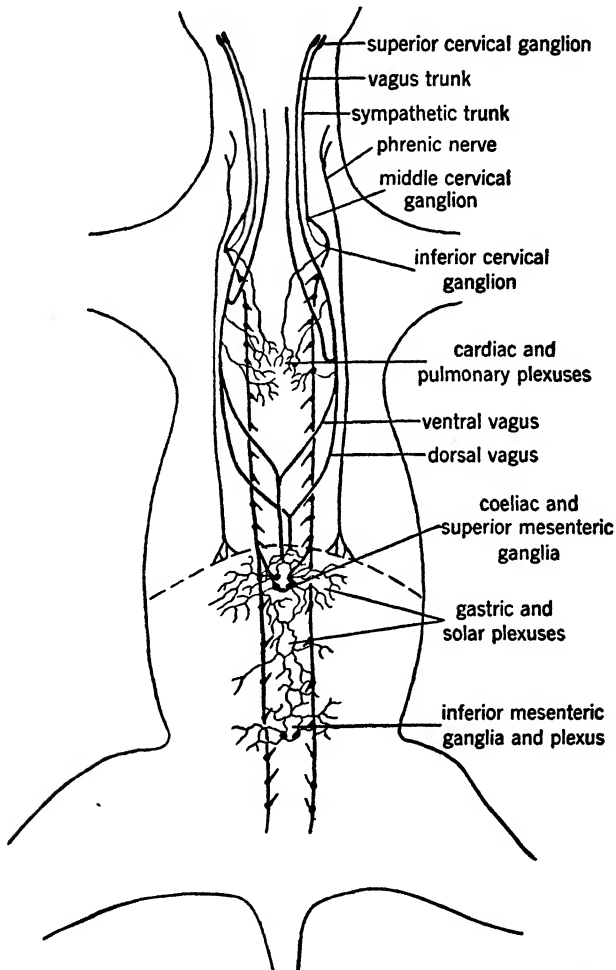


FIG. 314. Diagram of sympathetic system and associated nerves of a mammal.

antagonistic to those of the sympathetic system, and this double innervation is continued to all parts of the body, one set of fibers starting an action and the other set stopping it.

The sympathetic part of the system consists of a chain of ganglia in the head, neck, and body that are connected with the visceral ramus of the spinal nerves through a gray and white branch. In the head region

there is an irregular distribution of the ganglia, with no segmental arrangement. In higher vertebrates all these head ganglia are connected with the superior cervical ganglia and follow along the blood vessels, principally the carotid. The head ganglia consist of the ciliary, which supplies the ciliary muscles of the iris; the sphenopalatine, which supplies the blood vessels of the lining of the nose; the otic, which supplies the muscles of the ear structures; and the submaxillary, which supplies the submaxillary and sublingual glands. The ganglia of the neck consist of a fairly large superior cervical and a smaller median and inferior cervical. These cervical ganglia are connected with the head ganglia but also supply fibers to the body cavity, each sending a nerve to the heart and lungs.

Starting with the first thoracic and ending with the fourth sacral, two chains of ganglia (Fig. 314) extend along the vertebral column, supplying the organs and structures of the body. These have a segmental arrangement, and there is a pair of ganglia for each spinal nerve in this series, each ganglion being connected with the cord by a gray and a white branch. In man, this series consists of twenty-one ganglia. They are all connected by a pair of sympathetic trunk nerves which extend anteriorly to the superior cervical ganglion. In mammals two pairs of large ganglia, the semilunar and the superior mesenteric, are at the base of the superior mesenteric artery and send out nerves to form huge visceral plexuses. Another pair of ganglia on the inferior mesenteric artery form additional visceral plexuses.

The system is extended out to form a network around the organs, with concentrations of nerve material where there is a great deal of action. With few exceptions (bone marrow and the substance of the brain) these fibers extend to every part of the body. Plexuses placed at centers of action consist of the cardiac associated with the heart and lungs, several plexuses of the digestive organs and associated structures, and the pelvic plexus connected with the urogenital organs and other structures of the posterior part of the body.

The fibers of the autonomic system may be divided into two types, the pre- and post-ganglionic, the preganglionic fibers originating from the cells within the central system and the postganglionic fibers from the cells of the sympathetic system. Preganglionic fibers are medullated and pass through the white rami into the sympathetic ganglia. Postganglionic fibers are non-medullated and come from cells within the sympathetic ganglia. They pass to the smooth muscles by way of sympathetic nerves or to the body wall by the way of the spinal nerves, which they enter through the gray rami.

The chromaffin cells accompany the autonomic system in its withdrawal from the cord during embryonic development. They contain

epinephrin, a substance important in animal life. The hormones from these cells make possible the explosive action of muscles. In higher animals, these cells are in the adrenal glands.

The Brains of Various Vertebrates

There has been a gradual change in emphasis from the lowest vertebrates, in which the sense regions of the brain are large and prominent, to the highest vertebrates, in which the cerebral lobes are in complete control.

Brain of *Amphioxus*

The questionable brain of *Amphioxus*, consisting of only one vesicle, is smaller than the adjacent parts of the spinal cord and has but a single ventricle. The neuropore remains open throughout the life of the animal. The posterior region is differentiated from the anterior part and perhaps represents what is to be the deuterencephalon. The sensory centers are problematical, since the animal has no eyes and nothing to indicate a sense similar to hearing or equilibrium. The olfactory sense seems to be the most important. Cranial nerves are present, but it is impossible to homologize them with the nerves of the higher forms. The spinal nerves have two roots, which do not join as in the higher vertebrates. The relationship of the brain of *Amphioxus* to that of the vertebrates remains questionable.

Brain of the Cyclostomes

The brain of the cyclostomes is rather simple when compared to that of the shark, but it has the same general plan, although the divisions are not so well marked. Both the cerebral lobes and the cerebellum are quite small and undeveloped. Four ventricles are present, but the ventricles of the fore brain are not completely separated. The sensory parts of the brain serving the nose, eye, and ear are large and influence the shape of the brain as a whole. In *Petromyzontia*, the cerebellum is a small structure (practically absent in myxinoids) anterior to the fossa rhomboidalis, covering only a small area on the anterior part of the rhombencephalon. On the diencephalon of the petromyzonts, but not in the myxinoids, a double epiphyseal apparatus extends dorsally; the posterior structure is the pineal structure with a vestigial eye, and the anterior structure is the parietal structure with a vestigial parietal eye. A well-defined infundibulum appears on the ventral side of the diencephalon and bears a hypophysis (pituitary body). In *Petromyzon* (Fig. 10) the nasal pit extends posteriorly and ends in a peculiar pituitary sac next to the pituitary body. Ten cranial

nerves of fishes are present in the petromyzonts but only eight are located on the brain proper; the last two, corresponding to IX and X of higher vertebrates, are located outside of the skull. Myxinoids lack the optic nerve as their eyes are degenerate.

Brain of Fishes

The brains of the fishes are quite variable within the class (Figs. 311, 312, 315). The proportionate amount of brain tissue is small in comparison to the body weight. The brain of the fish is largely a sense

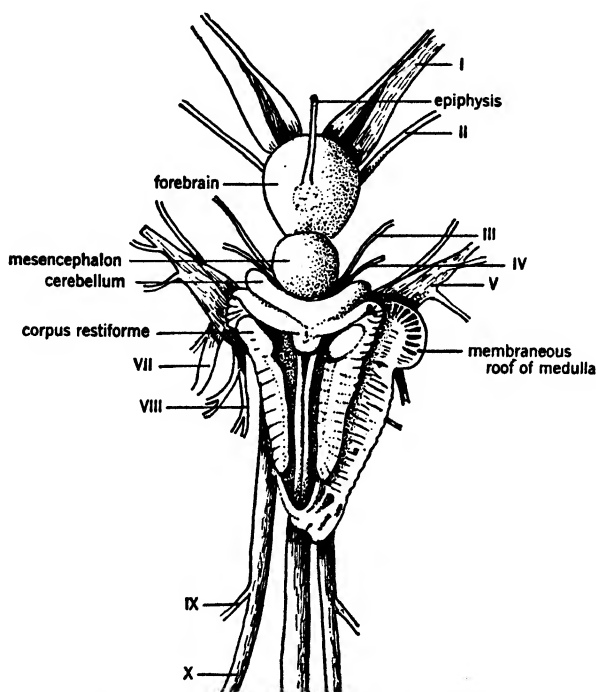


FIG. 315. Dorsal aspect of the brain of *Polyodon spathula*, with left side of roof of medulla dissected away. After Garman.

structure, with developments of nervous tissue for the regulation of smell, sight, and equilibrium. The roof of the telencephalon is not developed except in the sharks and Dipnoi, and the anterior part is not well connected with the rest of the brain. The olfactory lobes are always large and prominent, the eye lobes are out of proportion to the other parts, and the cerebellum is large and well developed. The pineal structure is prominent in the sharks, extending anteriorly to a small foramen in the chondrocranium; it is reduced in the teleosts, but it is well developed in the Dipnoi. Some ganoids or intermediate

fishes show evidence of a parietal eye in addition to the pineal structure. The cerebellum seems to vary with the habits of the animals, being large in the good swimmers and small in others. Enormous vagus lobes on the medulla (Fig. 312) develop in response to the sense of taste, as in the buffalo fish (*Ictiobus urus*). The fore brain of the Dipnoi resembles that of the amphibians in that the pallium is somewhat thickened and contains neurons. The fish brain is marked by a greatly enlarged corpus striatum. Fishes and amphibians have ten cranial nerves, the glossopharyngeal (IX) and the pneumogastric (X) having been added to the eight found in the lowest vertebrates.

Brain of Amphibians

The brain of the amphibians (Figs. 316, 317) is quite distinctive in that the telencephalon is larger, with a greater development of the pallium (cerebrum) and a reduction of the corpus striatum. The

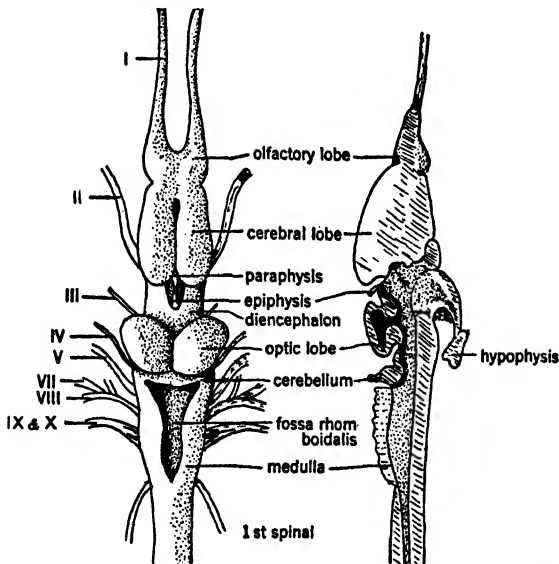


FIG. 316. Brain of frog (*Rana*). Dorsal and sagittal.

pallium is being invaded by neurons and is suggestive of what is to appear in the reptiles. The lobes of the telencephalon, as a rule, are distinct, although they are joined in the Anura. The olfactory lobes do not show distinct separation from the cerebral hemispheres. The cerebellum is small and poorly developed, but the optic lobes remain large. In the ancient amphibians, the parietal eye was very large, judging from the size of the parietal foramen, but in modern amphibians only a small pineal body appears.

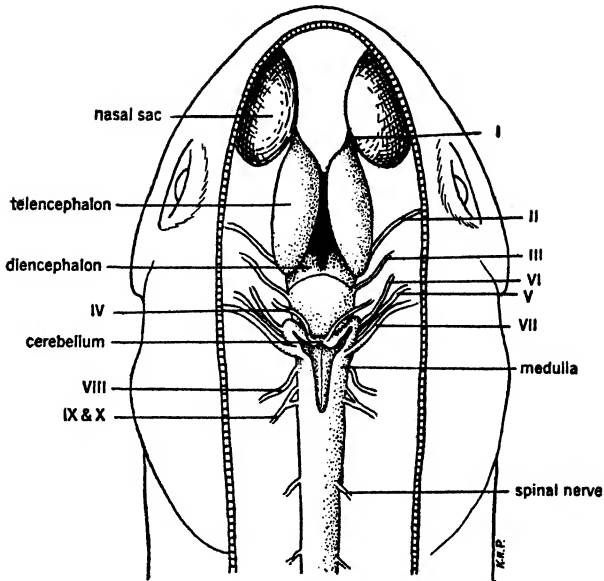


FIG. 317. Dissection of the brain of *Ambystoma*.

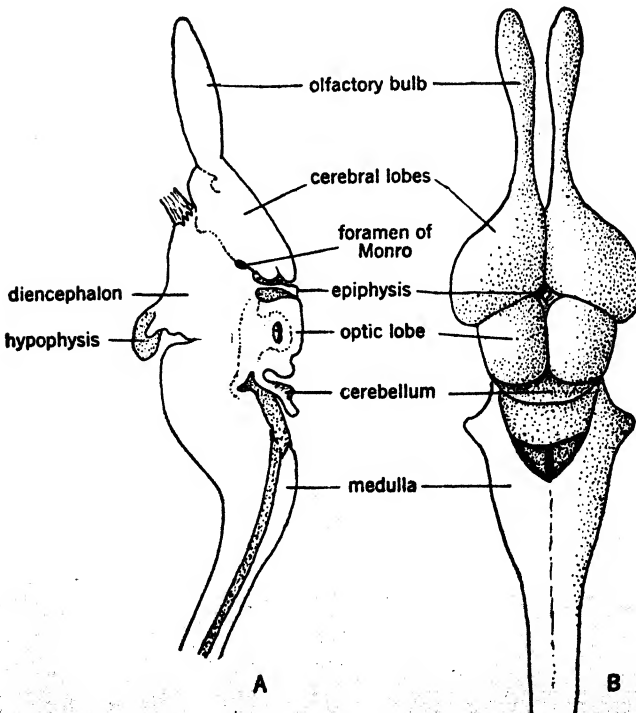


FIG. 318. Brain of snake (*Natrix*). A, sagittal section; B, dorsal.

Brain of Reptiles

The brain of the reptiles (Figs. 318, 319, 320) is a decided step in advance over that of the amphibians, both in structure and in proportionate size. There is a striking increase in the size of the telencephalon, which now becomes the largest region of the brain. Its anterior region is prolonged as a stalk, ending in an enlarged olfactory bulb from which the olfactory nerve is continued to the epithelium of the nose. The corpus striatum is enlarged, and the pallium (cerebrum) shows a marked increase in thickness and in the number of neurons contained. Consistent with the increase in size of the pallium, there is an added number of connecting tracts now continued forward from the posterior parts of the brain to this region. The cerebrum has grown posteriorly and partly covers the diencephalon.

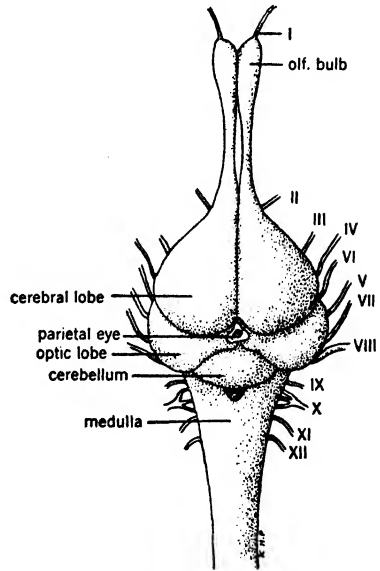


FIG. 319. Dorsal aspect of the brain of *Sceloporus*.

The parietal eye (Fig. 310) attains its best development in certain reptiles, being very prominent in *Sphenodon* and in most of the lizards.

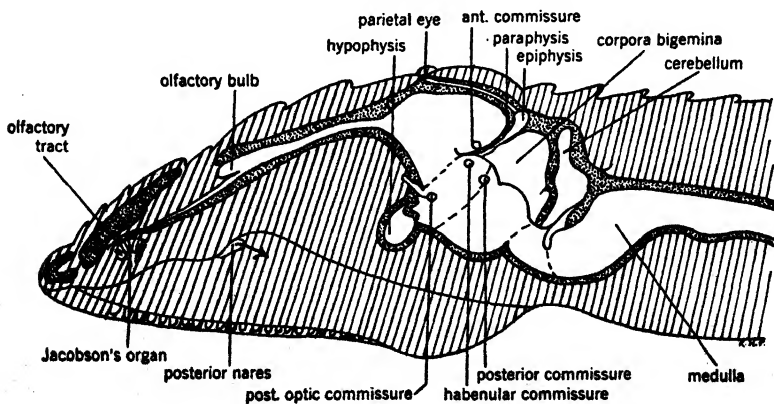


FIG. 320. Sagittal section of the head and brain in *Sceloporus*.

Some reptiles have both pineal and parietal structures, but usually it is the parietal body that persists. The infundibulum and hypophysis

continue to be well developed. The sensory structures are still large, but the emphasis is changing, and the region connected with the sense of smell is gradually being reduced. The eye and the ear have large brain centers. The mesencephalon has two large optic lobes, the corpora bigemina, which are forced laterally by the posterior growth of the telencephalon. The cerebellum is rather simple but is increasing in size and, with the additional flocculi in Crocodilia and other forms, is considerably larger than that of the amphibians.

There is no unusual development of the myelencephalon, which supplies the exits for the posterior cranial nerves. Two cranial nerves

have been added, the spinal accessory (XI) and the hypoglossal (XII), making a total of twelve not counting the terminal nerve. This number is continued in the birds and mammals. Although the brain is much improved over amphibian conditions, by a large increase in the number of tracts and connections with the anterior part, the proportionate size is still quite small, since the brain of a 200-pound alligator weighs but a fraction of an ounce.

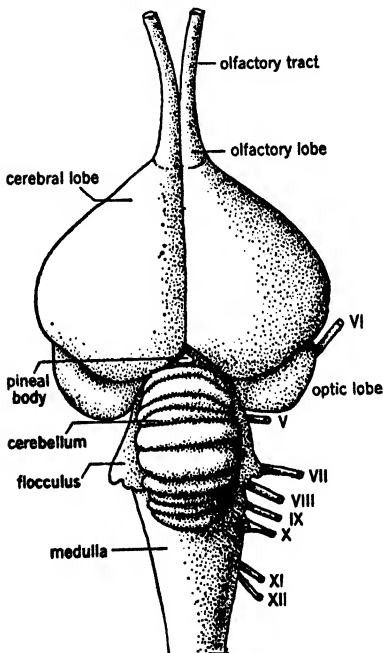


FIG. 321. Brain of chicken. Dorsal.

Brain of Birds

The brain of birds (Figs. 321, 322) is larger in proportion than that of the reptiles, being short and wide, with a greater development of the anterior lobes than in any of the lower vertebrates, and with more evident flexures. Since birds are highly specialized for flight, their brain has become highly modified along with the rest of their body. There is an increase in the size of some of its parts, with added nervous structures. The activity of the bird is correlated with a great increase in the size of the telencephalon. The olfactory region is reduced, being smaller than in the lower forms. The cerebral lobes are smooth, with no corrugations or furrows. The pallium is thin and not highly developed, but there is an increase in the number of neurons contained and also a number of new connecting tracts. The corpus striatum is much enlarged, and evidently important to the bird from the tracts con-

necting it with the posterior part of the brain. The lateral ventricles are slit-like, since they are encroached upon by the corpus striatum. As the cerebral lobes extend posteriorly to meet the cerebellum, the diencephalon and mesencephalon are not evident from the dorsal surface. The pineal body reaches the dorsal level of the brain by extending anteriorly through the angle made by the two cerebral lobes.

The diencephalon contains the slit-like third ventricle with two openings, the interventricular foramina, leading to the lateral ventricles. The roof is thin, with the epiphysis, or pineal body, extending anteriorly, and the choroid plexus dipping into the ventricle. Ventrally the optic chiasma is just anterior to the infundibulum. The hypophysis is quite distinctive and ventral to the infundibulum. As the side walls carry most of the tracts leading to the telencephalon, the thalamus is rather thick.

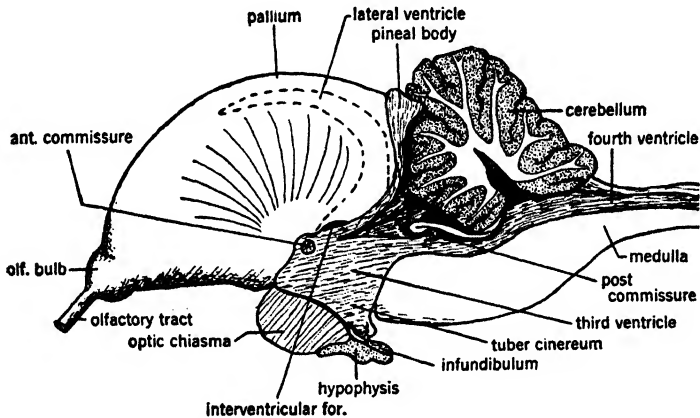


FIG. 322. Brain of chicken. Sagittal.

The mesencephalon is also covered by the overgrowth of the cerebellar lobes, and the corpora bigemina (optic lobes) are extended laterally, being larger and even more lateral than in the reptiles. A small tube, the iter, leads through the mesencephalon to connect with the fourth ventricle. The large posterior commissure is on the dorsal border on the anterior part of the roof. The optic nerves have their centers in the corpora bigemina and extend anteriorly from this region to the chiasma.

The cerebellum of the metencephalon is large and has a pair of flocculi on each side. The dorsal surface of the cerebellum is thrown into numerous folds, which increase its area, giving the bird a large number of brain cells for equilibrium. The pons is not developed in birds since only a few fibers cross from the sides of the cerebellum.

The medulla oblongata, or myelencephalon, is short, with a prom-

inent flexure and a large fossa rhomboidalis covered by a choroid plexus. It contains the fourth ventricle, and along its sides eight cranial nerves leave the brain.

The spinal cord extends to the pelvic region with large plexuses for the wings and legs, the thoracic plexus being especially large because of the amount of muscle tissue concerned with flight.

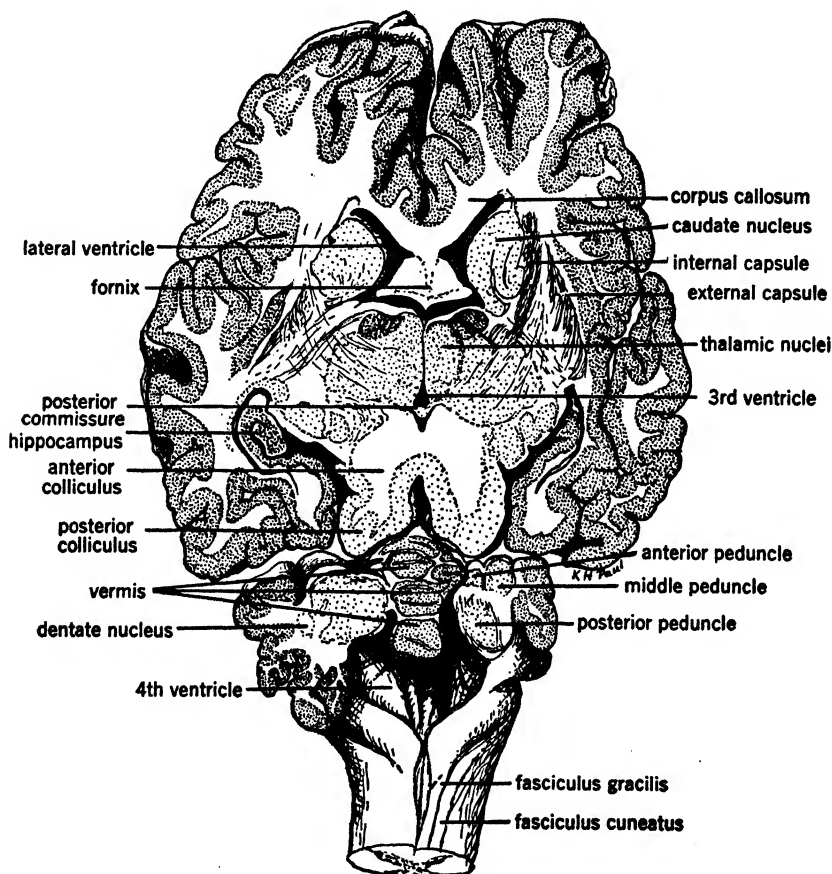


FIG. 323. Frontal section of sheep brain through posterior commissure and posterior colliculus. Natural size.

Brain of Mammals

The monotremes have a brain, with small smooth cerebral hemispheres, which is not much advanced over that of the reptiles. The marsupials develop a larger brain with much better developed cerebral hemispheres. The pons, a heavy commissure encircling the ventral stem of the metencephalon, appears. The brain of the placental mam-

mals shows the greatest development in both size and structure. (See Figs. 323, 324, 325, 326, 327.) Proportionately, it is much larger, and there is a difference in the relative development of the divisions. The cerebral lobes now become the predominating structure, and there has been an enormous increase in the number of tracts and interconnections necessary to make its functioning possible. The cerebral and cerebellar lobes are so enlarged that the other divisions seem small in comparison. The cerebral lobes are formed principally by the greatly thickened

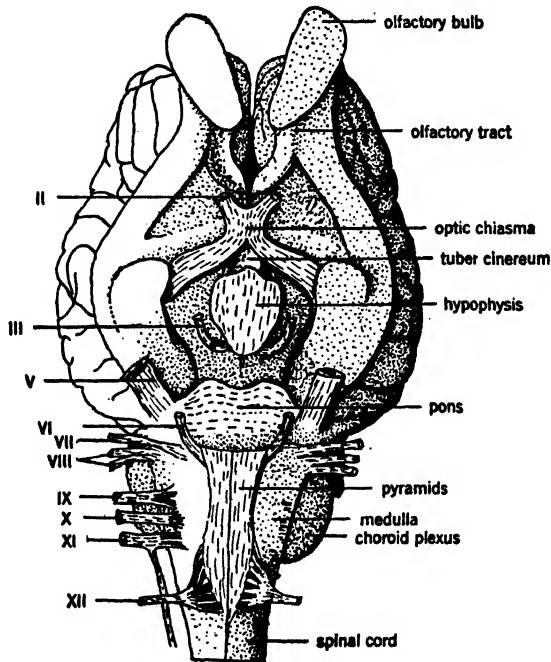


FIG. 324. Brain of sheep. Ventral. After Sisson.

pallium with its increased mass of neurons. The surface is smooth in many mammals, but there is a tendency to increase the surface area of the cortex by folding and by the formation of sulci and gyri. The corpus callosum, the major connection between the cerebral lobes, is a new development. Many other connecting tracts are developed, so that the cerebrum becomes the dominant part of the brain, with centers concerned in every activity of the animal. The cerebral lobes are so enlarged that they completely cover the diencephalon and mesencephalon. In some placentals such as the carnivores, ungulates, and primates the cerebrum is much convoluted, increasing the surface and the superficial layer of gray matter.

The optic lobes now appear as four bodies instead of two, as the

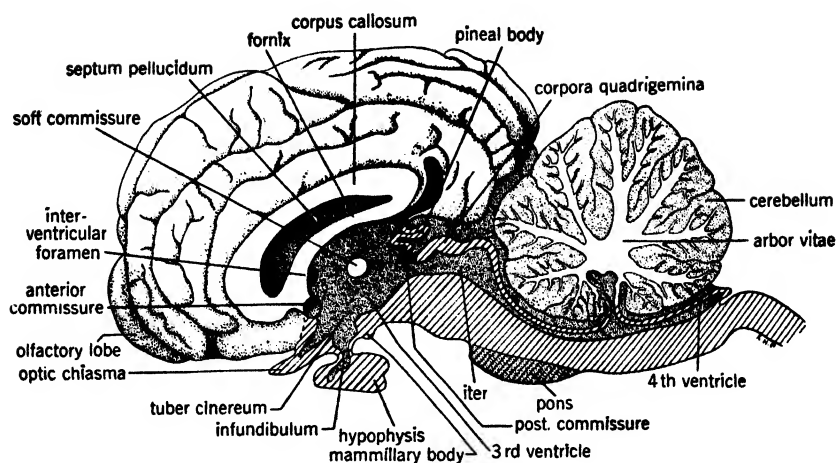


FIG. 325. Sagittal section of mammal brain, diagrammatic.

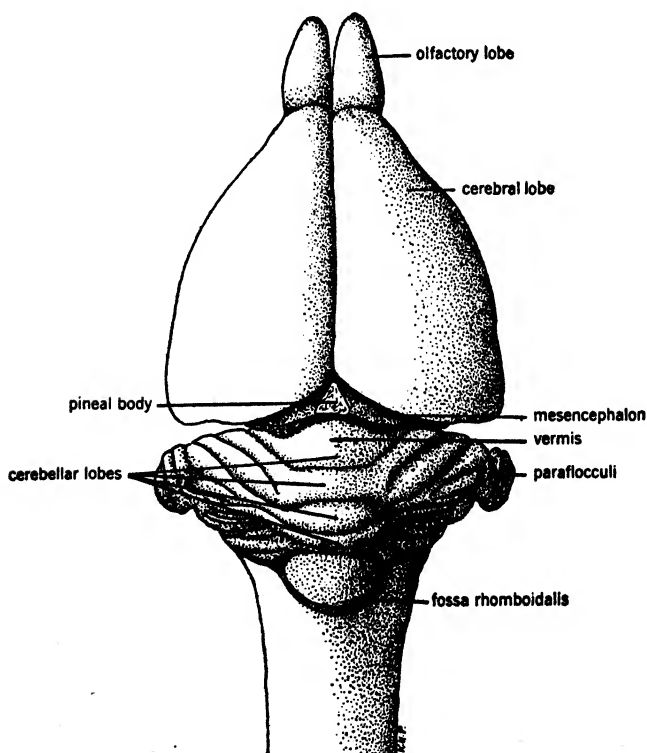


FIG. 326. Brain of white rat. Dorsal.

corpora bigemina now have a transverse groove, forming the corpora quadrigemina. The cerebellum has developed large, lateral lobes and is greatly improved by the addition of the pons, a connecting commissure already mentioned. No great change has occurred in the medulla.

The covering of the brain is in three layers: the outer layer, or dura mater, which lines the brain case, is tough and fibrous; the middle layer, arachnoid, is light and vascular; and the inner layer, or pia mater, is applied closely to the brain, in contact with all its surface.

The dura dips down between the lobes of the cerebrum, forming a

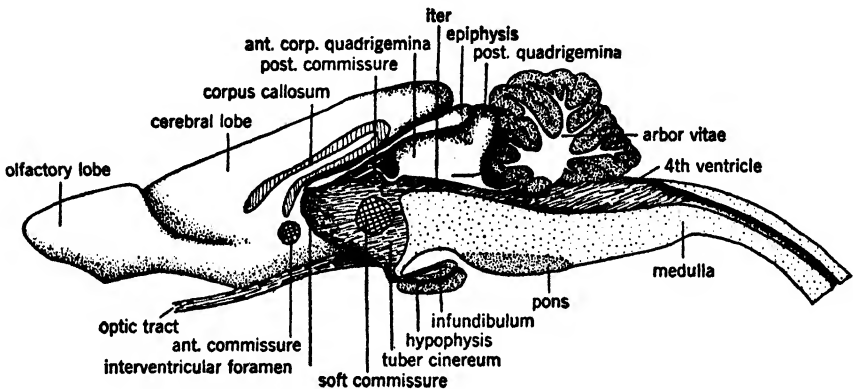


FIG. 327. Brain of white rat, sagittal section.

thin plate, the falx cerebri, which may become osseous. The dura also dips down between the cerebrum and cerebellum, forming another dividing plate, the tentorium, which also may become osseous. Four ventricles are present, two in the cerebral lobes, one in the diencephalon, and one in the myelencephalon. The fourth ventricle in the myelencephalon has pushed forward until it lies partly under the cerebellum.

The olfactory lobes at the anterior end of the telencephalon are quite reduced and are pushed into a ventral position by the heavy growth of the cerebral hemispheres. In sagittal section, the corpus callosum, a new structure connecting the cerebral lobes, is quite prominent, and the septum pellucidum and the fornix also appear clearly. The anterior commissure is located at the lower end of the fornix. The interventricular foramen (foramen of Monro) is a narrow slit, located at the ventro-posterior region of the fornix, and connects the third ventricle with the lateral ventricles. The tracts connecting the posterior part of the brain are not conspicuous in a sagittal section but appear in stained cross sections. The corpus striatum, in the ventral region of the telencephalon, is much smaller than in birds.

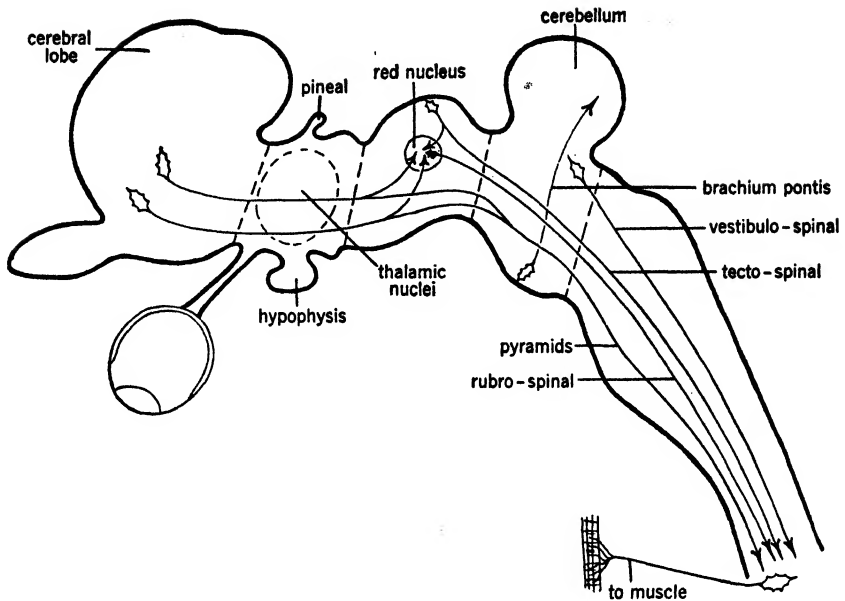


FIG. 328. Diagrammatic representation of some of the main outgoing or motor tracts of the mammalian brain.

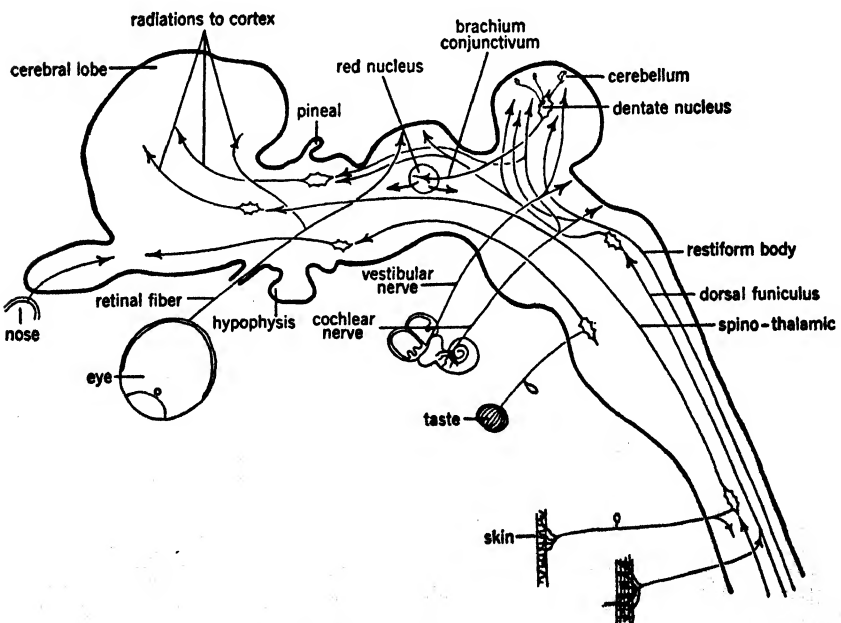


FIG. 329. Diagrammatic representation of some of the main incoming or sensory tracts of the mammalian brain.

The diencephalon (Fig. 327) does not appear in a dorsal view but is clearly defined in sagittal section. Its antero-ventral region is the exit of the optic nerves. Posterior to the chiasma, the infundibulum extends as a blind pouch along the ventral surface and is surrounded by the hypophysis. On the dorsal wall, an epiphysis, the pineal body, extends between the cerebral and cerebellar lobes. The posterior commissure marks the separation of the diencephalon and mesencephalon. Extending through the slit-like third ventricle is a large soft commissure, the commissure mollis. Most of the connecting tracts must pass through the walls, or thalami, to get to the different parts of the brain.

The mesencephalon (Fig. 327) is also covered, so that it is not visible from the dorsal surface. The dorsal wall is divided into four lobes, the corpora quadrigemina, concerned originally with the sense of sight but now also a center for the sense of smell. The iter is a small tube connecting the third and fourth ventricles. The ventral region forms the brain stem for the transmission of the tracts passing through it. A thin velum separates the dorsal wall from the cerebellum.

The metencephalon (Fig. 326) is a large structure, as in birds. Two new cerebellar lobes have been added, making this division different from all other vertebrates below the mammals. The cerebellum consists of the vermis, the new cerebellar lobes, the lateral flocculi, and the mushroom-like paraflocculi, which extend into a pocket in the side of the brain case. The pons is a U-shaped band connecting the two halves of the cerebellum. The connection with the mesencephalon is by means of a pair of anterior peduncles, and the connection with the myelencephalon is by means of a pair of posterior peduncles.

The posterior medullary velum separates the metencephalon from the myelencephalon. The large fossa rhomboidalis is covered by a choroid plexus, which extends down into the fourth ventricle and forward under the cerebellum. The posterior peduncles must curve around the fossa to reach the cerebellum. Centers controlling respiration, circulation, and digestion are in this section of the brain.

There are twelve pairs of cranial nerves in all mammals.

CHAPTER SIXTEEN

Sense Organs

Animal life is protected by its sense organs, and its central system is kept informed of outside occurrences by sets of receptors that have become specialized to deal with particular stimuli. Land animals have retained many of the receptors common to water life, but they have also added new ones during their adjustment to a land habitat.

The sense organs consist of a series of simple and complex receptors originally developed from ectodermal cells. The primitive receptors end in the skin, but these may be withdrawn within the body wall and

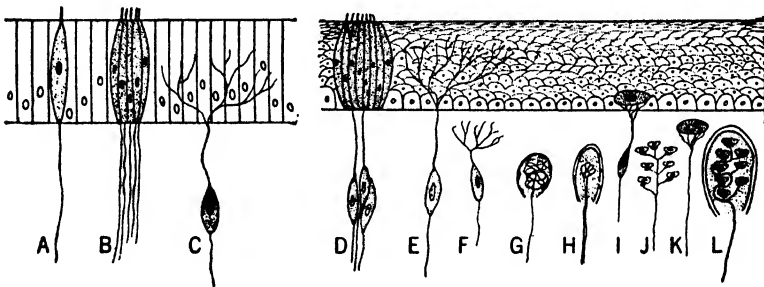


FIG. 330. Diagram of epidermal sense organs in chordates. *A-C*, primitive sense cells of acranians; *D-L*, sense cells of vertebrates. *A*, single sense cell; *B*, sense bud; *C*, free nerve endings in epidermis; *D*, sense bud; *E*, free nerve ending in epidermis; *F*, free nerve ending in corium; *G*, sense cells with nerve fiber wound in a capsule; *H*, encapsulated sense cell; *I*, epithelial tactile cell; *J*, group of tactile cells in corium with no capsule; *K*, tactile cell in corium; *L*, encapsulated group of tactile cells in corium. After L. Plate.

may acquire numerous accessory parts. The simplest end organ is a nerve itself which spreads out in a network close to the surface, among the epidermal cells of the skin. Many specialized cells are found in the skin, for the perception of heat, cold, pressure, etc.; and specialized end organs of sense cells are found in the lateral line, eye, nose, ear, and taste buds. Interiorly, special cells for receiving stimuli are found in the muscles, joints, and tendons, and in the digestive organs for the perception of hunger, thirst, pain, etc. No animals, however, are

known to have developed sense receptors for the perception of certain radiations, such as X-rays, which have harmful effects on the body.

It seems probable that all specialized cells have developed from unspecialized touch receptors, or nerves that were generalized in their reception of stimuli of various types, chiefly by contact. Early in the history of the vertebrates, and before that time in the invertebrates, these cells became specialized. Several developments were necessary to existence, especially in those senses connected with food-getting. Thus taste and smell were developed early in animal life, with sight following closely. The organs of equilibrium developed in the invertebrates and were probably present in the first vertebrates. The temperature receptors were also important, since many aquatic animals have narrow temperature limits. The sense cells of the lateral line and the ear mechanism are probably related, since their functions are somewhat similar. In the adjustments to land life, the olfactory organs were modified, the eye changed to a longer range of activities, and acute hearing was added to the sense of equilibrium.

Simple Sense Cells

Besides the highly specialized and organized sense structures, such as those for sight and hearing, single sense cells and small groups of sense cells (Fig. 331) are scattered over the surface and in the deeper

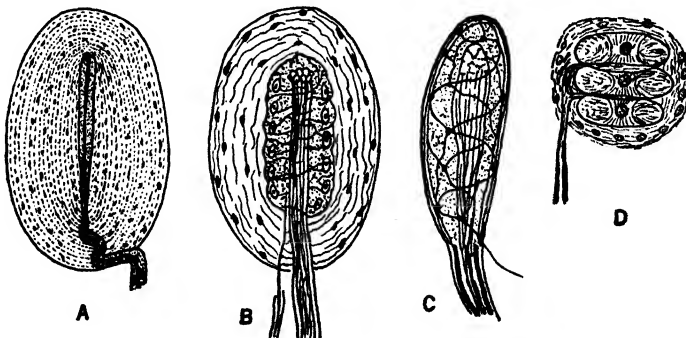


FIG. 331. Sense corpuscles of different types. A, Pacinian corpuscle from the mesentery of a cat (after Bohm, Davidoff, and Huber); B, Herbst's corpuscle from the tongue of a duck (after Plate); C, Krausse's corpuscle (after Bütschli); D, Grandry's corpuscle (after Bütschli).

parts of the body that are associated with other sensations. These may consist of plain nerve endings or of rather complicated special end organs, or corpuscles. Specialized receptors are found in the skin, especially on parts of the body that are modified for special uses, as the bills of some birds, the nose of the mole, the snout of the pig, etc.;

and also in the conjunctiva of the eye, in the taste buds, and in the cells of the lateral line (Fig. 332). Other receptors may be merely naked nerve endings among the epidermal cells. Inside the body, in tendons, joints, bones, teeth, and mesenteries, a second series of receptors function to provide for the needs of each region.

Neuromasts

Some rather simple sense organs, called neuromasts, are found in the skin of cyclostomes, fishes, and water-living amphibians. Each of these epidermal sense organs consists of a few sensory cells connected with nerve fibers and protected by a number of non-nervous supporting cells (Fig. 332). They may be single, or a number of them

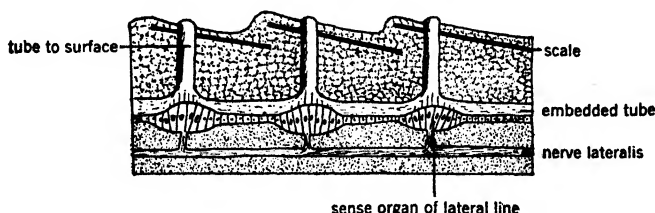


FIG. 332. Lateral line, diagrammatic. Modified from Kingsley.

may combine to form a series. Typically they are found in regular lines near each eye (suborbital, supraorbital, and infraorbital lines) and in a lateral line continuing along each side of the body to the tail region. They may sink into the skin and form ampullae, grooves, or canals, but each neuromast has its individual opening. The ampullae of Lorenzini, found in sharks, are in clusters close to the lateral-line organs and have the same innervation. The vesicles of Savi are found in some elasmobranchs, on the head and around the electrical organs. These ampullae and vesicles are filled with a clear jelly and are called slime organs. Their function is probably to register changes in pressure.

The lateral line, a special development of fishes and amphibians, consists of a series of sensory patches, usually imbedded in the skin, forming lines around the eyes, over the head, and along the side of the body (Fig. 332). It is supposed to be concerned in the recognition of low vibrations in water. Other functions have also been assigned to it. The origin of the lateral-line system and the associated slime organs is from the dorsolateral placode of the embryo, and the auditory pit originates from this same structure. This placode elongates, both anteriorly and posteriorly, and supplies the material for the canals on the head and lateral line in fishes and amphibians. The innervation is very characteristic and is constant in animals with these structures. The cranial nerve facialis (VII) is the one most closely associated with

the canals on the head; the glossopharyngeal (IX) and the vagus (X) supply the lateral line with a nerve (lateralis of vagus) extending along the whole length of the body. This system and its nerves are completely lost in the land animals (Fig. 332) above the amphibians.

Organs of Taste

The sense of taste is limited to testing materials that are sour, sweet, bitter, and salty. It is important for food-finding in the lower forms and for food-testing in the higher. The sense buds are skin organs, very similar to neuromasts in their structure, and they function only in moisture. The sense cells are contained in flask-shaped structures with sensory hairs projecting out of the flasks.

Taste buds are scattered along the sides of the body and on the head in many fishes. Some fishes, such as bullheads, have special barbels around the mouth supplied with taste organs. Land animals have taste cells confined to the tongue, the circumvallate and foliate papillae, the lips, and parts of the throat. The innervation of the taste buds is generally by the glossopharyngeal nerve (IX), but there are variations.

Olfactory Organs

Smell is one of the most primitive, as well as one of the most important, of the primary senses. The nose is situated anterior to the mouth and is innervated by the olfactory nerve and the terminal nerve. In the early vertebrates the anterior part of the brain is concerned almost entirely with the innervation of this structure. In fishes the olfactory region (rhinencephalon) is relatively large, but in amphibians, reptiles, and birds it gradually becomes reduced, and in mammals it is completely overshadowed by the great overgrowth of the cerebral hemispheres.

The nasal pit lies within a blind sac in all fishes except the Choanichthyes. Land-living vertebrates draw the air used in respiration over the olfactory area before it passes to the lungs, thus assuring a constant sampling of the air. As all odors must be dissolved in the fluids of the sense organs, there is little difference, fundamentally, between the method of detecting odor in fishes and land vertebrates. The cells for receiving the sensation are close to the surface and send impulses to the neurons of the olfactory lobes by way of the olfactory tract which is a tract of the brain rather than a nerve in the ordinary sense.

Smell and taste are similar, but, whereas the sense of taste is much restricted in its scope, the sense of smell is almost unlimited in its powers of discrimination. The detection of odors in the air is a great source of protection to land animals, both in guarding them from their

enemies and in helping them to find food. The testing of food is also carried on by this sense.

The olfactory organ is a paired structure in all vertebrates except the cyclostomes, in which it is single. The nose arises from epidermal placodes that are invaginated and drawn in to form shallow pouches, which in most fishes have no connection with the mouth. The Choanichthyes have the nasal pits opening into the mouth through internal nares. The amphibians have the same arrangement with the internal nares opening into the anterior part of the mouth. In reptiles a secondary shelf begins to close off the roof of the mouth and to drive the internal nares to the posterior. In Crocodilia and Mammalia this shelf drives the nares far back by the formation of a hard palate, a secondary structure built up by median extensions of the palatine and maxillary bones.

Nasal Structure in Cyclostomes

The cyclostomes have a single nostril but have two olfactory nerves, which indicate that in all probability the original structure was paired. The nasal sac is close to the hypophysis, and a passage extends ventrally to a blind sac just anterior to the hypophysis. In development the invaginations forming the hypophysis and the nasal pit are close together but are not identical. Later the two pits deepen and are gradually drawn into the skull on the ventral side, and finally the growth of the enormous funnel forces the depressions to the dorsal surface of the head.

Nasal Structure in Fishes

The nasal structure of all fishes has the form of a pair of blind nasal sacs, not connected with the mouth except in the Crossopterygii and the Dipnoi. The blind sacs usually have a flap across their openings, forming incurrent and excurrent apertures, which cause the water to flow in and out of the sacs, as the fish swims about. The nasal pits of the shark (*Squalus*) are enclosed in cartilage to form thin-walled capsules. The olfactory nerves enter the capsules and spread over the membranes, thus forming the olfactory surface of each nasal pit. This inner membrane is thrown into folds attached to the periphery of the capsule and anchored by a septum. The folds are innervated by the olfactory nerve.

Nasal Structure in Amphibians

The amphibians inheriting the nasal structure of their crossopterygian ancestors, have their nasal capsules opening internally into the roof of the mouth (Fig. 207). This arrangement with some modifica-

tions is retained in all the higher vertebrates. Surrounding the nasal capsules of the amphibians are cartilaginous pouches as in the fishes. The external nares of the Anura close after the air is taken in, so that the air can be forced into the lungs by the action of the throat muscles. The internal nares are small and just posterior to the dental ridge in the Anura. The tear duct and Jacobson's organ, a pit opening into the nasal passage, first make their appearance in the amphibians.

Nasal Structure in Reptiles

The reptilian nasal structure (Fig. 333) is a stage in advance of the amphibians, having additional parts and being better adapted for land life. The development of the accessory foldings starts with the reptiles, by the development of a bony conch on the ventral and lateral walls of the nasal passage. The internal nares open in the roof of the mouth. There is a division of the nasal chamber into two parts, an anterior respiratory and a posterior olfactory portion. The tear gland discharges into the narial passage by a small duct. Jacobson's organ (Fig. 333), a pit in the narial passage, is well developed in most reptiles and is especially prominent in the lizards. In some reptiles it moves from the nasal passage to the mouth and seems to be associated with taste. It is absent in turtles and crocodiles.

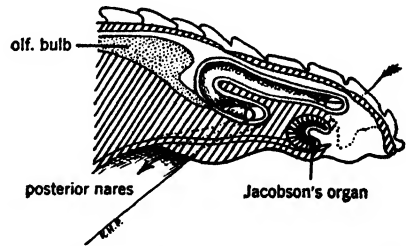


FIG. 333. Sagittal section of the nose of *Sceloporus*.

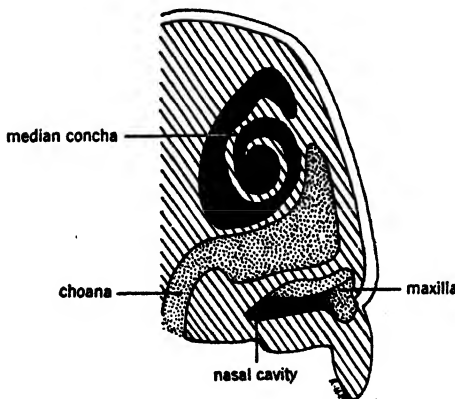


FIG. 334. Cross-section of nose of chicken.

forming a scroll. There is the same division of the nasal passage into a respiratory and an olfactory chamber. The internal nares open into single or double slits in the roof of the mouth and may be divided by a septum. The sense of smell is fairly well developed in some birds, but in general it is their weakest sense, since their sight and hearing are so much more acute. The organ of Jacobson is absent.

Nasal Structure in Birds

The olfactory organs of birds (Fig. 334) resemble in most respects those of the reptiles, although the conch is generally more complicated,

Nasal Structure in Mammals

The mammals have the greatest development of the sense of smell and have the most specialized nose found in the vertebrates. Turbinal scrolls, or conchae, develop on the sides of the narial cavity, thus increasing the surface exposed to the air. The lower anterior part is the respiratory chamber, used to warm and wash the air coming through

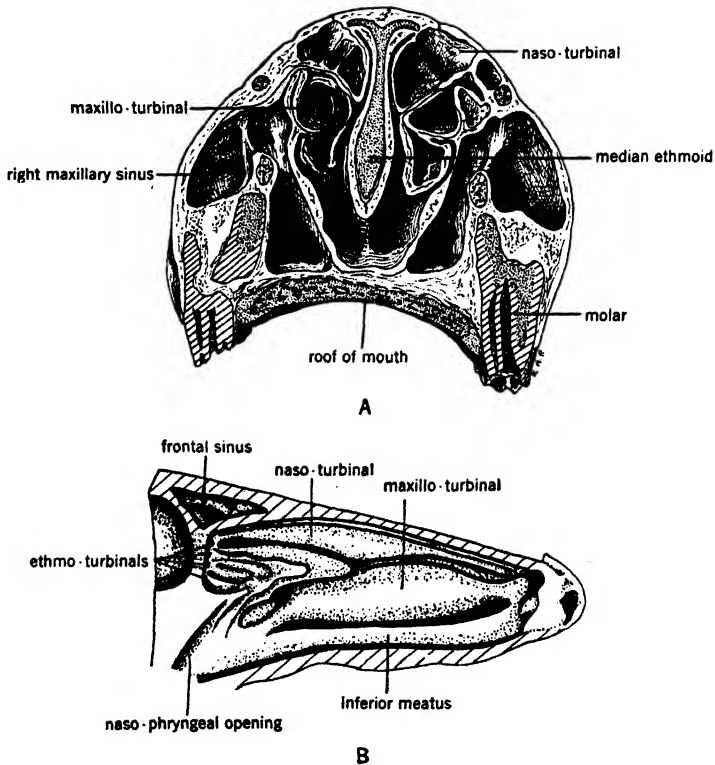


FIG. 335. *A*, cross-section of nose of a cow (original); *B*, sagittal section of a calf nose. After Weber.

on its way to the lungs. The upper posterior part of the passage is devoted to the olfactory sense, and the nerves of the olfactory tract reach the areas of smell through the cribriform plate of the ethmoid bone.

The bony elements supporting the turbinal are the naso-, maxillo-, and ethmo-turbinals. These elements may be greatly subdivided and developed from the nasals, maxillae, and ethmoids. A number of sinuses, extending into the frontals, maxillae, and sphenoid, may develop in connection with the nose. The sinuses may be lined with olfactory mucous membrane in those animals with the highest devel-

opment of the sense of smell, but in other animals they may have nothing at all to do with this sense (Fig. 335).

Jacobson's organ (Figs. 320, 333), which originates in amphibians from a small specialized portion of the nasal cavity, is in direct connection with the nose in mammals. In reptiles it is quite complex and has a duct of its own connecting with the mouth. Certain mammals, such as the monotremes, marsupials, edentates, ungulates, and rodents, have a well-developed Jacobson's organ with an opening into the mouth through the incisive foramen. In bats, aquatic mammals, man, and other primates, the organ develops in the young but is lost in the adult, although the foramen incisivum persists as a vestige.

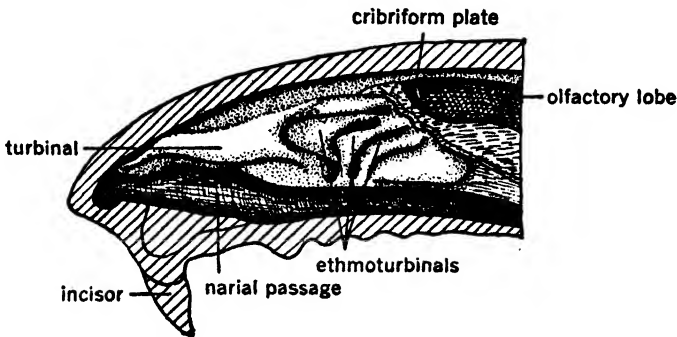


FIG. 336. Nose of white rat, sagittal section.

The external nose is practically a mammalian characteristic, and it is subject to many variations. A median plate-like cartilage supports the structure and at the same time renders it flexible, while the inner framework formed by the turbinals makes the organ effective. The specialization of the nose to form additional sense structures appears in moles and shrews, where it is tactile in addition to its usual function. Greatly extended noses are found in ungulates and in the elephants, with the formation of a trunk that becomes a prehensile organ.

The Ear

The primitive ear of the vertebrate corresponds to the inner ear of mammals and is found in all vertebrates. It consists of a membranous sac-like structure from which one to three semicircular ducts arise. It functions as an organ of equilibrium and of hearing. The semicircular ducts are largely concerned with equilibrium.

Lampreys have two ducts and hagfishes have only one duct, but the single duct of hagfishes may consist of two fused ducts. All other vertebrates have three semicircular ducts. They are arranged so as

to detect any change of position in relation to gravity; two of them are perpendicular and one horizontal. All ducts are suspended in canals imbedded in the skull. They are filled with a fluid, endolymph, in which are suspended small bodies of some sort. In fishes these bodies are usually small calcareous structures or otoliths (Fig. 341) except in some sharks, where the endolymph duct remains open and allows sand grains to enter. In these sharks the ear may be filled with sea water instead of endolymph. Small calcareous crystals (otoconia) take the place of otoliths in the land vertebrates. Each of the ducts is enlarged at one end, to form an ampulla (Figs. 337, 350), in which there is a sensory patch, or crista acustica, covered

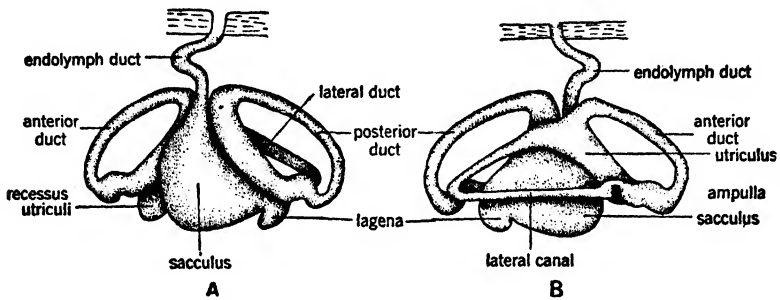


FIG. 337. Membranous ear of *Squalus acanthias*. *A*, mesial of right ear; *B*, lateral of right ear. After Retzius.

with hair-like projections from the receptors. Any change in the position of the body causes movement of the endolymph and otoliths, which strike the sensory hairs in the crista acustica. The sensation thus originating is transmitted through the fibers of the auditory nerve tract to the medulla and thence to the cerebellum, the part of the brain primarily concerned in equilibrium.

Development starts with an auditory placode, which becomes invaginated and finally drawn into the head in the region of the first gill cleft. This invagination forms a pit with a duct that opens to the outside and is retained in the sharks as the endolymphatic duct (Fig. 337). This vesicle develops ridges that separate off, to form a lumen, and develop into the semicircular ducts. The utriculus, sacculus, and lagena are parts of the primitive ear of the lower forms, the utriculus being the body of the sac from which the ducts were originally pinched off, while the rest of the vesicle develops into a sacculus and a second prolongation, the lagena, which is to become the cochlea of the mammals (Fig. 337 *A, B*). The whole mechanism is very small and condensed and is enclosed in the walls of the skull.

The sacculus and lagena are the parts of the ear chiefly concerned

with hearing. These parts have little or no differentiation in the cyclostomes but begin their development in the fishes, by the addition of accessory parts and by the formation of the cochlear branch of the auditory nerve. This development is associated with a number of

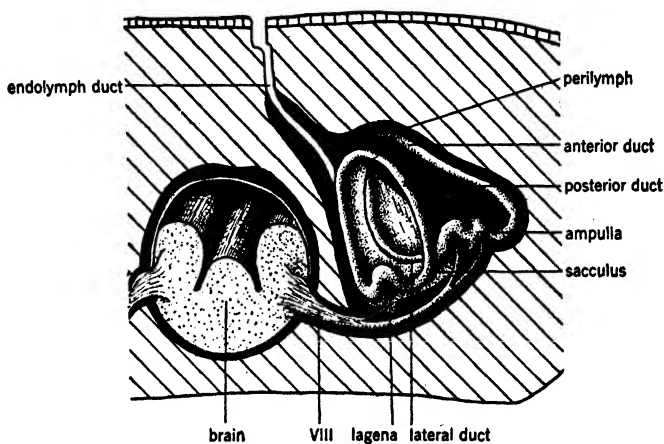


FIG. 338. Ear of shark as seen from the posterior.

important changes in which the ducts and utriculus become slightly separated from the sacculus and the beginning cochlea. This separation becomes more marked as the differentiation progresses in the vertebrates. The middle ear, with its two drums and a plunger, the stapes, appears first in the amphibians.

The Ear of Various Vertebrates

Fishes

In fishes nothing but the inner ear is developed, and, although equilibrium is its main function, fishes can hear very well with this structure. The receptors consist of the cristae acusticae (Fig. 351) in the ampullae, and the maculae acusticae on the other parts. The sacculus and other parts of the ear, with these sensory patches, seem to be the seat of hearing. In many teleosts such as the drum (*Aplodinotus grunniens*), (Fig. 340) the otoliths become quite large and are called ear stones (Fig. 339). They show rings of growth and can be used to determine age. Some of the bony fishes have a tube connecting the swim bladder with the ear. The Ostariophysi have the Weberian apparatus, consisting of a chain of bones that connect the swim bladder with the ear and probably register the air pressure of the bladder (Fig. 267).

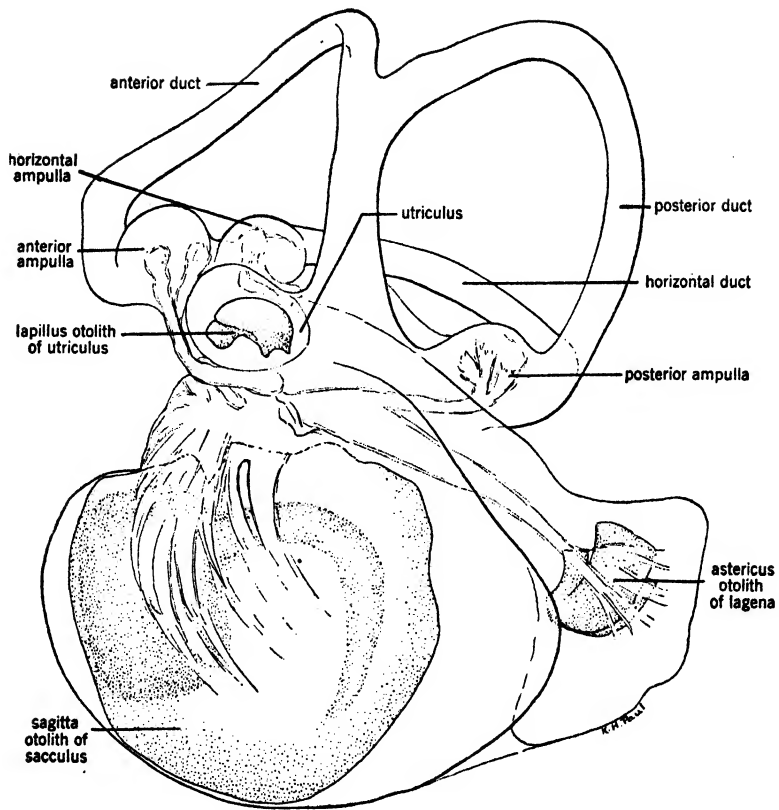


FIG. 339. Membranous right ear, mesial aspect, of the drum, *Aplodinotus grunniens*.

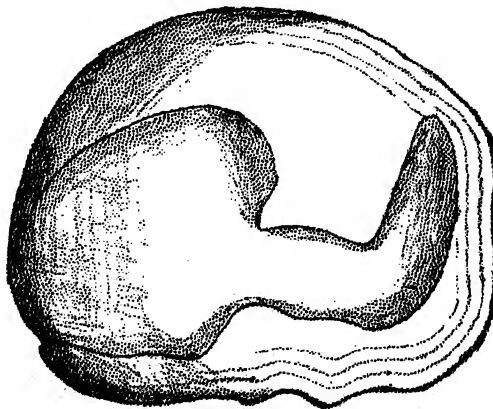


FIG. 340. Otolith of the sheephead or fresh water drum, *Aplodinotus grunniens*.

Amphibians

The ear of the amphibian (Figs. 342, 343) is a land structure, with accessory parts that make it able to function in the air. The greatest change is the addition of the middle ear formed from the first gill cleft (spiracle) and retaining an opening into the pharynx through

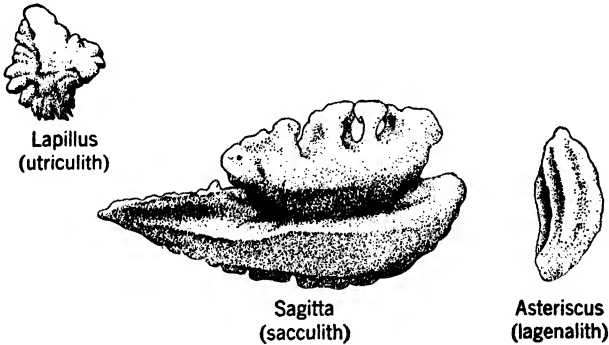


FIG. 341. Otoliths of the pike, *Esox lucius*. Left side.

the Eustachian tube, or tuba auditiva. A tympanic membrane, or ear drum, is formed over the external aperture by the failure of the first gill cleft to break completely through in the embryonic development. The stapes (Figs. 343, 344), which develops from the hyomandibular bone of the fish, has passed into the cavity of the middle ear and acts

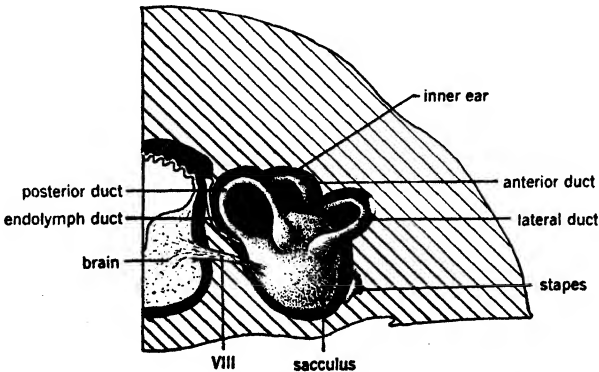


FIG. 342. The ear of *Ambystoma* as seen from the posterior.

as a plunger, connecting the inner ear with the tympanic membrane. The stapes of the amphibian consists of a basal plate, which fits into the foramen vestibuli of the inner ear, and is more or less fused to a rod, the columella or plectrum (Fig. 343). The origin of the plectrum is uncertain; it is thought by some to originate from the wall of the

otic capsule. The combined stapes and plectrum form the columella auris and serve to conduct sound vibrations from the tympanum to the inner ear. In amphibians, the inner ear is imbedded in cartilage or bone of the otic capsules and otherwise is similar to that of the fishes. The lagena is slightly longer than that of fishes. The middle ear and Eustachian tube are lost in the urodeles, as they possess only a membrane inner ear. The stapes is buried in the muscles of the jaw in *Ambystoma*, but in *Necturus* it articulates with the squamosal.

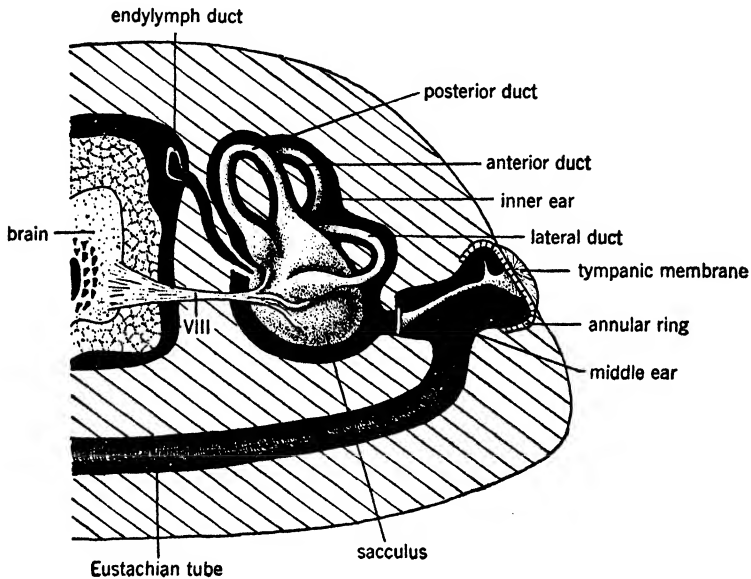


FIG. 343. Ear of frog as seen from the posterior.

Reptiles

The external auditory meatus or depression of the tympanic membrane begins to appear in the reptiles (Fig. 345), although the snakes have their tympanic membrane entirely covered by scales. The middle ear is on the same general plan as in the anurans. The inner ear shows some additional development in the lagena, which is elongated and curved, and in the basilar membrane, which replaces the papillae lagena. The lagena of the higher reptiles begins to resemble the mammalian cochlear structure. The lagena attaches itself to each side of the bony canal and thus forms three ducts: a median duct (the original lagena), the scala media filled with endolymph; a dorsal duct, the scala vestibuli; and a ventral duct, the scala tympani, both filled with perilymph (Fig. 350). See page 434.

In the middle ear there is a further development of the columella

which consists of the stapedial plate, a columella auris, and an extra-columella, connecting the fenestra vestibuli with the tympanic membrane. The tuba auditiva, or Eustachian tube, is large and connects with the mouth through a wide opening. Both the endolymphatic and

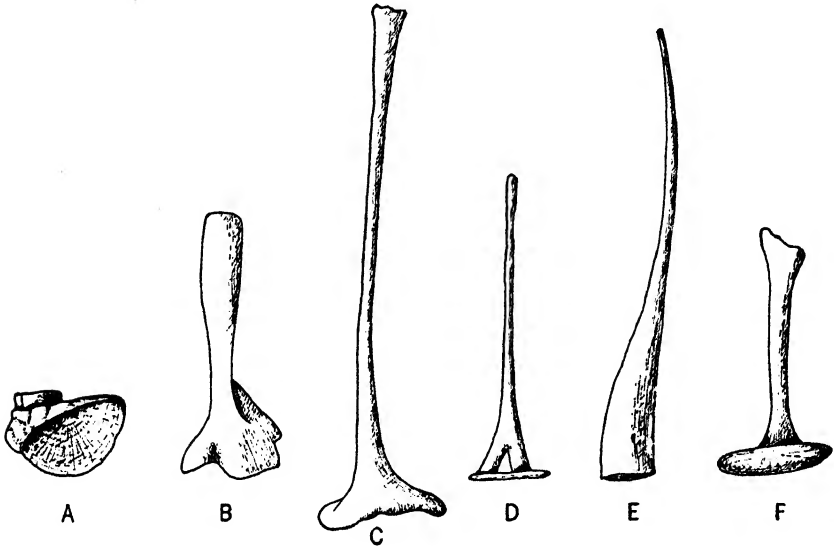


FIG. 344. Types of the columella auris. A, *Necturus*; B, frog (*Rana catesbiana*); C, turtle (*Chelydra serpentina*); D, alligator; E, sea-turtle (*Thalassochelys*); F, duck (*Anas*).

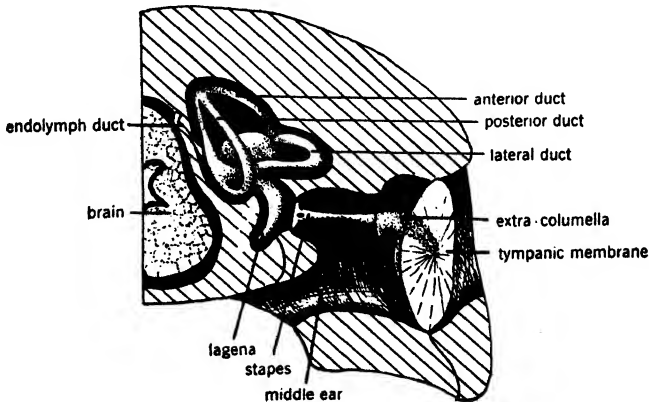


FIG. 345. Ear of reptile as seen from the posterior.

the perilymphatic ducts have formed connections with the lymph spaces in the meninges of the brain. The external meatus is shallow and protected only by its surrounding walls. (In the crocodiles there are flaps that suggest the outer ear of the higher animals.)

Birds

The ear of birds is highly developed, and superior to that of the reptiles (Fig. 347). The whole structure is housed in cancellous bone. The external meatus, which is always open, is curved so that the tympanic membrane is well protected, and a glandular worm-like ridge

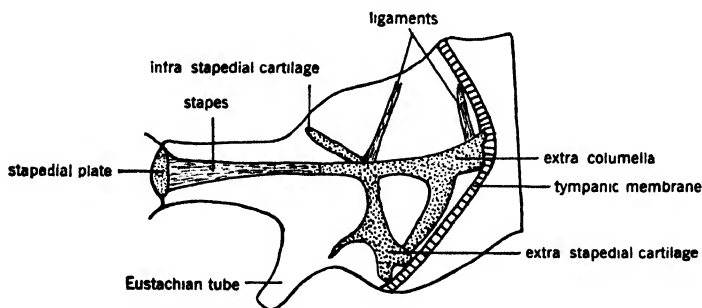


FIG. 346. Middle ear of chicken. Redrawn from Büchli.

extends along the floor of the meatus. A few birds (owls) have the outer meatus provided with movable flaps that serve as pinnae, with a protecting fringe of hair-like feathers. The tympanic membrane is held in a convex position by the extracolumella. The middle ear is small

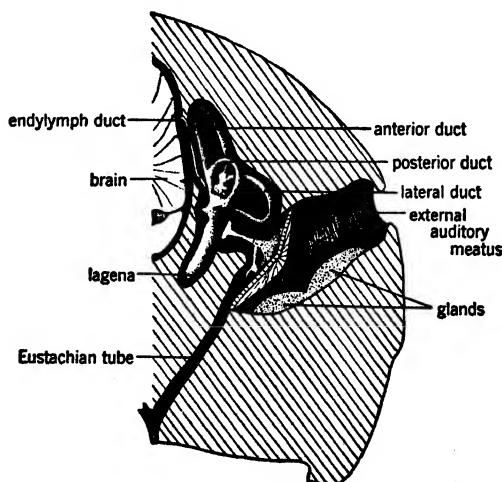


FIG. 347. Ear of bird (*Gallus*) as seen from the posterior.

and has a permanent Eustachian tube. The tubes unite and open to the roof of the pharynx by a single median slit. The ossicles of the ear consist of the stapes, with its plate fitting snugly into the foramen vestibuli. The columella (Fig. 346) extends as a long slender bone from the

stapedial plate and is continued to the tympanic membrane by the extracolumella, an irregular piece of cartilage which is attached to the tympanic membrane at several places. The ear has a very well-developed lagena, containing an organ of Corti, which evidently does the work of the same organ in mammals. The anterior semicircular duct is large, but the utriculus and the sacculus are rather small in proportion.

Mammals

The ear of the mammals (Fig. 348) is more highly developed than that of the reptiles. It has developed three parts: the outer (external) ear, the middle ear, and the inner (internal) ear. The ear is more

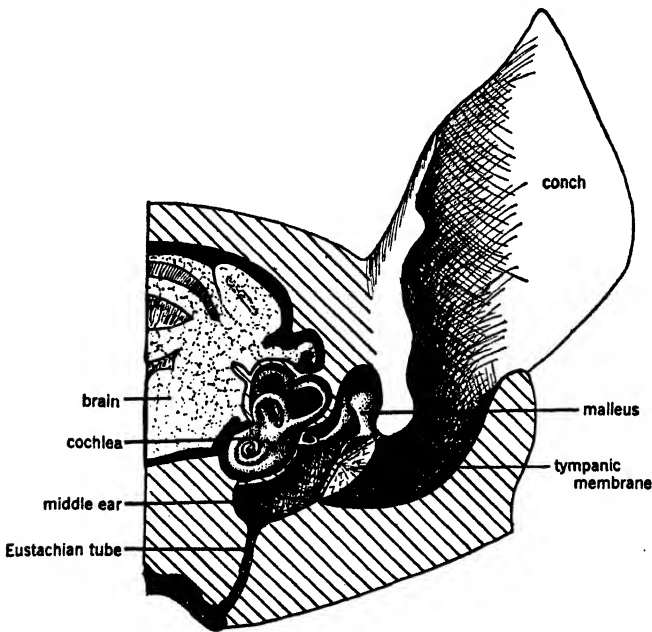


FIG. 348. Ear of mammal (rat) as seen from the anterior.

deeply imbedded in the skull and has added an outer accessory structure known as the external ear. The middle ear has added two more ossicles and now contains three ossicles: the stapes, incus, and malleus. The inner ear has become more complicated by the continuation of the growth of the lagena which was initiated in the reptiles.

Inner Ear of Mammals. The semicircular ducts (Fig. 353) of the mammals remain much as in the reptiles but are more firmly encased in very hard bone, the ivory-like periotic or petrosal. The separation of the ducts and the utriculus from the sacculus and the cochlea

becomes more pronounced, and there is only a small duct connecting them (Fig. 353 *A, B*). The membranous ear (Fig. 353 *B*) is filled with endolymph and is surrounded by the perilymph which transmits sound waves to the inner ear by the connection through the stapes. The endolymph and perilymph have connections with the subdural spaces around the brain, so that they are able to renew their fluids. There is a clear separation of the auditory nerve into two branches (Fig. 353 *B*): the vestibular branch, with two rami innervating the semicircular ducts, utricle, and saccule; and the cochlear branch, innervating the cochlea and the basilar membrane.

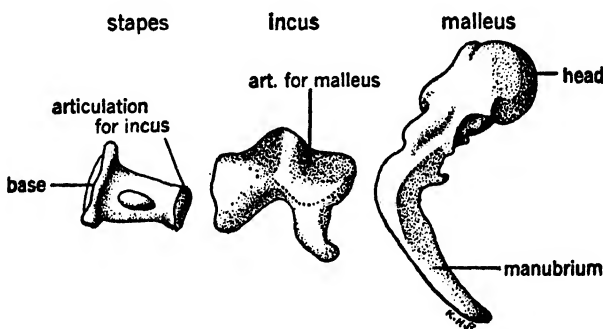


FIG. 349. Ossicles of mammalian ear.

The lagena (Fig. 353 *A*) has given rise to the cochlear duct, which is a membranous duct coiled inside the bony cochlea, and attached at each side to the cochlear wall, forming two other ducts, the scala vestibuli and the scala tympani (Fig. 350 *A, B*), both of which are filled with perilymph. The lagena itself, now called the scala media, has a highly specialized structure, the organ of Corti, which is the essential organ of hearing. Its floor is the basilar membrane; its roof, Reissner's membrane. The tectorial membrane transmits vibrations to the hair cells. The cochlear nerve extends along the modiolus, or core of the cochlea, and its branches enter the basal membrane and innervate the receptors, or hair cells. A tunnel extends the length of the organ, supported laterally by the outer and inner pillar cells. Deiter's cells (Fig. 352) extend from the membrane to the hair cells and act as supports. Henson's cells (Fig. 352) also serve as supports and are probably not to be considered as sense cells. Two windows open into the inner ear from the middle ear, the foramen vestibuli (foramen ovale) and the foramen tympani (foramen rotundum) (Fig. 353 *A*).

The stapes fits snugly into the foramen vestibuli, acting as a plunger to transmit the sound waves to the perilymph. The foramen tympani, or round foramen, is a release valve, covered with a membrane. It re-

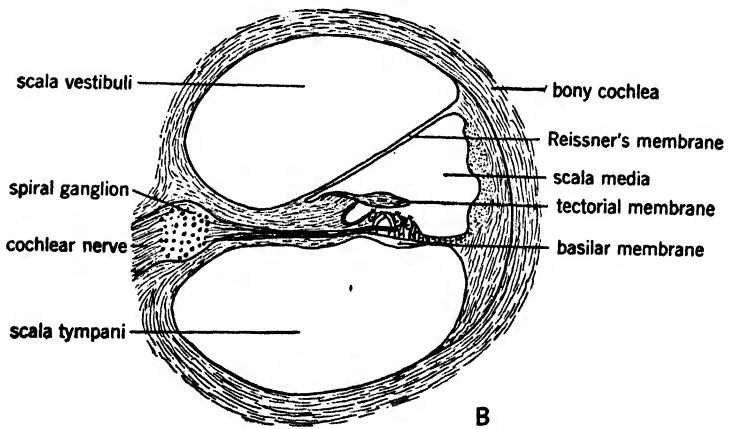
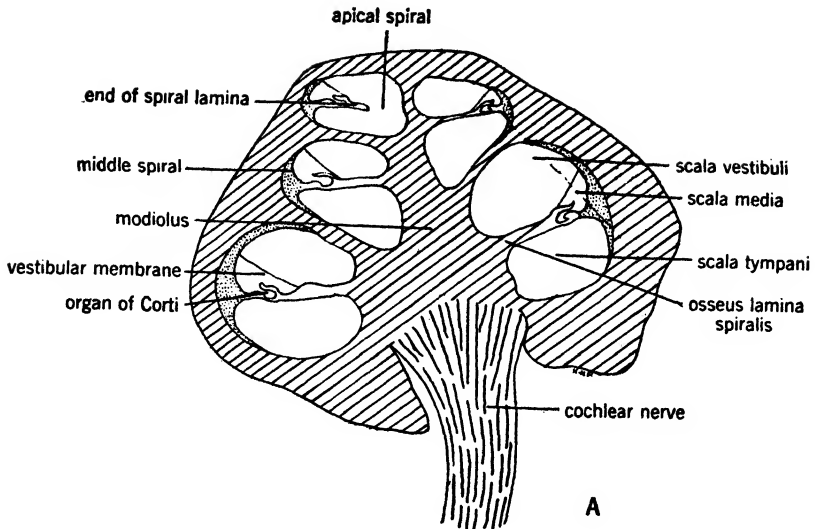


FIG. 350. *A*, section of cochlea of newborn child (after Plate); *B*, section through cochlea. After Bütschli.

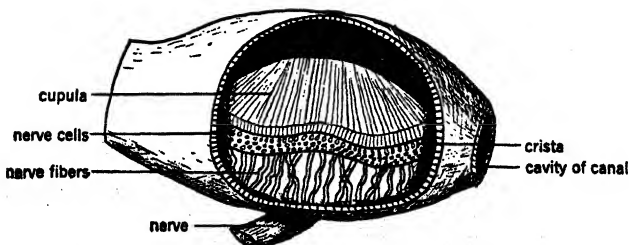


FIG. 351. Ampulla of semicircular duct, dissected to show structure. After Retzius.

lieves the pressure of the inner ear when the stapes is in action. Several theories have been advanced to explain the action of the organ of Corti (Fig. 352), and how sounds are received in the structure of the cochlea. One view has been that sounds enter any part of the cochlea and that a redistribution of the impulses is made in the brain. A second view, and one that appears to have the support of scientific investigation, is that the parts of the organ of Corti are localized and that tones are received in their appropriate focus of response. Experiments show that the high

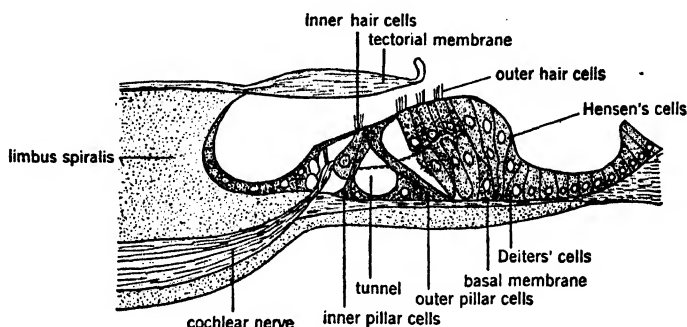


FIG. 352. Organ of Corti. After Retzius.

tones are received at the base of the cochlea and the low tones at the apex. Experiments on the easily exposed cochlea of the guinea pig, consisting of boring holes at definite parts of the spiral of the cochlea and then studying the results on hearing, seem to give favorable evidence for the localization theory. Animals in which parts of the organ of Corti have been destroyed show a definite loss of certain regions of the hearing band. Experiments of the same type, but using electrical contacts so that no part of the ear was injured, gave the same results. By these methods it was possible to map the cochlea of the guinea pig and mark the limits of the tone scale reception, and approximate the spot at which the different tone bands were received.

Middle Ear of Mammals. The middle ear, formed from the first gill cleft, is a relatively small air-filled chamber (Fig. 353 A) that is connected with the throat through the tuba auditiva (Eustachian tube), and closed at the outer auditory meatus by the tympanum or ear drum. This chamber contains the three ossicles, the mechanical parts through which vibrations are transmitted to the inner ear from the tympanum. Sound conduction of a coarser sort is also possible through the bones of the skull. The stapes (Fig. 349) is the hyomandibular portion of the columella auris and is the only part of this structure retained by mammals. It is the innermost of the three ossicles, is so placed that it closes the foramen vestibula, and is thus in communication with the fluids of

the inner ear. The movement of the stapes is of the pumphandle type rather than like a plunger. The stapedia muscle, a small slip, is attached to the neck of the stapes thus stabilizing its movements. The free end of the stapes articulates with the incus, and there is a small cup on the end of the stapes for this joint (Figs. 349, 353 A). The middle ossicle is the incus, formed from the quadrate of the reptile. The incus

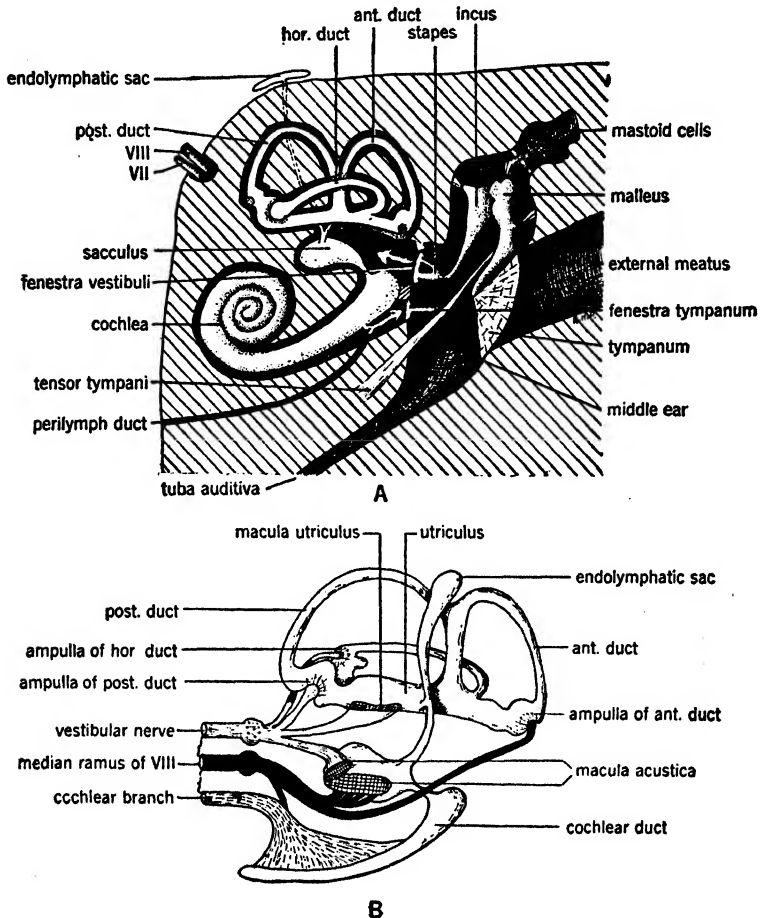


FIG. 353. A, diagrammatic section of mammalian ear; B, the membranous inner ear. After Weber.

is somewhat anvil-shaped and has two limbs or processes, the ventral articulating with the stapes. A slight protuberance articulates snugly with a reciprocal cup on the stapes. This articulation of the incus is sometimes free instead of joined and is called the lenticular bone when separate. There is a good lenticular in the rat. The ossicle is attached to the wall of the inner ear by a ligament. A depression on the body

of the incus supplies the articulating facet for the head of the malleus (Figs. 349, 353 A).

The malleus or outer member of the chain of ossicles, is the largest of the three, and makes contact with the tympanum or ear drum. It is derived from the reptilian articular and consists of a head, two arms, and usually an anterior process. The head fits into a facet on the incus, which is probably the original mandibular articulation of the reptile. The arms are attached to the tympanic membrane. The tensor tympani muscle (Fig. 353 A), which takes its origin in the wall of the tuba auditiva, extends to the lower limb or manubrium and serves as a regulator of the tenseness of the drum. The drum is tensed for faint or indistinct tones and loosened for loud noises that might injure the drum.

Outer Ear in Mammals. The outer ear, or pinna, is foreshadowed in the Crocodilia, where a movable scaly flap may open or close over the external meatus. A similar apparatus found in some birds (owls) consists of a fold of skin acting in the same manner. The pinna of the mammals is a cartilaginous conch composed of material borrowed from the pharyngeal cartilages of the lower forms. It is present in all mammals, but for obvious reasons it is greatly reduced in water and burrowing forms.

The Eye

The eyes of all vertebrates are homologous structures, differing only in minor details, since an eye is just as useful in water as on land and no great change is required in the development of one from the other. Eyes of land vertebrates developed focusing lens, glands to keep the surface moist, and movable lids to protect them. Primitively, the sense organs affected by light rays were located in the skin and independent to some extent, but in the evolutionary process they were taken deeper into the body and buried in mesoderm, later to extend again to the surface, as shown by embryonic development. The vertebrate eye is indirect in the sense that the rods and cones, or light-perceiving sense cells, are directed posteriorly and are not struck directly by the light rays; this is in contrast to the direct eye of the invertebrates in which the receptors are pointed towards the source of light.

Embryology

The eyes of the vertebrates originate from three embryological sources: the ectoderm of the brain, the ectoderm of the outer body wall, and the mesodermal mesenchyme cells. The retina develops from the walls of the diencephalon, although the anlage can be shown in the

medullary plate. This plate follows the walls of the brain in its infoldings and outfoldings, and finally its position is fixed on the wall of the diencephalon as the beginning of the retina, with its receptors pointing toward the brain. The diencephalon pushes out an optic cup on each side. The inner surface of the cup thickens and becomes the sensitive surface of the retina; the outer or posterior wall of the cup forms the pigment layer of the retina. The rim of the cup gives rise to part of the iris, and the stalk becomes the optic nerve. A fissure remains on the ventral side, so that the optic cup is not perfect, and through this notch extend the ganglia of the nerves from the optic tract and the blood vessels of the eyeball. The lens originates as a thickening of the ectoderm over the optic cup, which sinks in and is cut off, and its concentric structure results from the growth of the cells in regular layers around this center. Mesenchyme cells form the choroid and sclerotic coats about the eye.



FIG. 354. Chiasma of the optic nerves. A, most fishes; B, herring; C, lizard; D, mammal in which the fibers from one nerve go to both eyes. After Wiedersheim.

Eye Structure

The eyeball of all vertebrates is covered by a light-colored tough coat, the sclera, which is continuous over the front of the eyeball, where it is transparent, forming the cornea for entrance of light. The black choroid coat is under the sclera and does not extend over the front of the eye but turns inward to help form the iris. The iris is a circular diaphragm enclosing an opening, the pupil. The iris is usually pigmented, mammals having three layers of pigment cells. By expanding or contracting the pupil, the iris controls the amount of light entering the eye. Its sphincter and dilator muscles are innervated by the autonomic system.

The innermost coat is the gray retina, which lines only the back part of the eye and consists of nerve cells, nerve fibers, and light receptors (Figs. 355, 356). The lens is a crystalline spherical or biconvex structure, suspended just behind the iris and the pupil. It focuses the light and resulting image on the sensitive retina. The lens is held in place by the choroid coat, which becomes part of the ciliary process, the ciliary muscle (Fig. 360), and the suspensory ligament known as the zonula ciliaris. In fishes and amphibians the lens is spherical, and the accommodation (or focusing of the image on the retina) is through

slight back and forth movements of the lens. Most vision under water is short-distance, and little accommodation is needed. In the higher vertebrates the lens is biconvex, and the accommodation for near and far vision is by changes in the shape of the lens itself, through the action of the ciliary muscle and process.

There are two chambers (Fig. 360) in front of the lens: the anterior chamber, which is between the iris and the cornea; and the posterior chamber, which is between the iris and the lens and is limited by the ciliary process. These two chambers communicate with each other through the pupil and are filled with the aqueous humor. The eyeball proper (posterior to the lens) is filled with the jelly-like vitreous humor. The fluids of the eye are supplied through the lymph system.

The optic nerve, really a tract of the brain, leaves the back of the eyeball and carries nerve fibers to the brain from the retina. The optic nerves of fishes cross each other to form a chiasma (Fig. 354), but there is no intermingling of the fibers from one eye with those from the other at this crossing point. In higher vertebrates the fibers from the optic nerves may split partially at the chiasma, so that those from each eye are conducted to optic centers on both sides of the brain. The eyeball can be rotated in any desired position by means of three pairs of muscles previously described (p. 246, Fig. 194).

Retina. The retina (Fig. 356), which is the sensitive lining of the eyeball, is derived from nervous tissue; it consists of a layer of nerve fibers, several layers of nerve cells, and a layer of rods and cones, the specialized light-receptors, the ends of which are imbedded in a layer of pigment cells. The nerve fibers, coming in from the optic tract, are spread in a network over the surface of the retina and thus make up the first layer through which the light passes. The ends of these fibers penetrate the deeper layers of the retina, forming connections with the nerve cells and granular cells that compose these layers, and finally reach the sensitive rod-shaped and cone-shaped receptors (Fig. 355). Since the rays of light must go through all these layers to reach the receptors, the intervening structures must be perfectly transparent.

The "blind spot" of the retina is the point of entrance of the optic tract, since this area lacks rods and cones. The macula lutea is a yellowish spot on the retina near the posterior pole of the eye. Within the macula is the fovea centralis (Fig. 359), which is a thin spot on the retina where some of the layers are missing and where the rods are especially numerous and vision is most acute. The retina extends outward intact and ends in a wavy line, the ora serrata, where it ceases to be nervous.

The tapetum lucidum, a thin shiny layer of pigment cells, is developed on the choroid coat next to the retina in some fishes, carnivores,

and other animals. It is very conspicuous in the domestic cat when exposed to a bright light at night. It is silvery in fishes, so that their

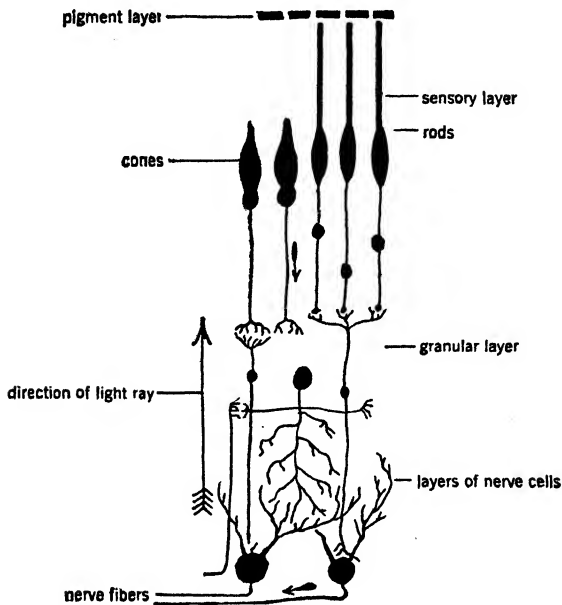


FIG. 355. Structure of retina. After Morris.

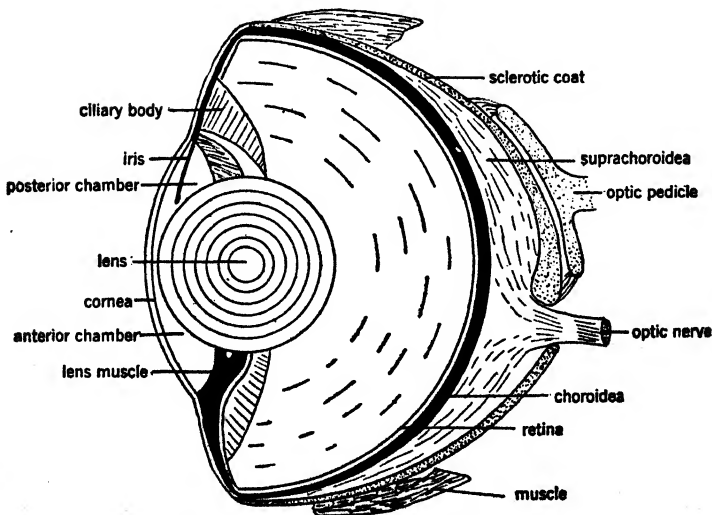


FIG. 356. Eye of shark (*Squalus acanthias*). After Franz.

eyes have a metallic color. It is supposed to aid vision in weak light. The visual purple is a pigment developed in the rods which fades on exposure to light. It is possible to get a photographic image by expos-

ing an eye that has been in the dark and fixing it immediately in an alum solution.

Choroid Coat. The choroid coat (Fig. 359), which surrounds the retina and forms part of the iris, is a highly vascular mesodermal layer, rich in blood vessels and lymph spaces. It is black and serves to absorb light.

Sclera. The sclerotic or outer coat (Fig. 359) is tough and fibrous and may contain bone. Sclerotic ossifications occur in all classes except the mammals. Bony sclerotic rings appear to be a protection to the eye, in preventing any change of shape under pressure, and they seem particularly valuable to water animals and birds. The optic tract and blood vessels must pierce this coat to reach the interior of the eyeball. The sclera covers the entire eyeball, forming the thin transparent cornea on the front. The cornea is covered by a very thin layer of epidermis, continuous with the skin of the lids, which forms the delicate conjunctivum.

Accessory Eye Structures

The eye of land vertebrates is so sensitive that it must be protected in every way to preserve its efficiency. The eyelids, found in most land vertebrates, consist of a pair of movable flaps that close and permit the shutting out of light. Lids do not appear in the fishes but are found in all the other classes. In snakes the eyelids are grown together and cleared, so that the eye is shut permanently. The lids with their glands prevent drying of moist parts and supply fluid lubricants. The eyebrows and eyelashes contribute to protection from foreign matter. The nictitating membrane, a third eyelid, is prominent in lower animals, but in the mammals it is reduced to a small rudimentary structure in the inner angle of the eye, the *plica semilunaris*.

The glands of the eye, the Harderian on the inner angle and the lacrimal on the outer, are developed with land life. These glands are not present in fishes and are rather small in amphibians, but become highly developed in reptiles, birds, and mammals. They are usually lacking or rudimentary in water-living forms of even the higher classes. Fluids from these glands are spread over the eyeball by the moving of the lids, the excess being carried to the nasal cavity through the lacrimal duct, which has two openings, the superior and the inferior, at the inner angle of the eye. The Meibomian or tarsal glands (modified sebaceous glands) spread a thin film of oil along the borders of the lids and thus aid in preventing overflow of the fluids. The ciliary glands open along the borders of the lids.

The falciform process found in some fishes extends from the retina to the lens and aids in accommodation. The pecten (Fig. 358), or

comb, found in some reptiles and birds, is thought to be homologous to this process. The pecten is a peculiar, folded, fan-like body that extends out from the retina at the entrance of the optic tract, and in some birds comes in contact with the lens. It has been suggested that the pecten aids in stabilizing the internal pressure of the eyeball rather than in accommodation of the lens.

The modifications of the eye are correlated with the many different uses of the structure. Telescopic types develop in some deep-water fishes, where the vision must be difficult, and birds of prey have eyes modified to meet the need of a very keen sense of sight. *Anableps*, a peculiar fish that spends much of its time at the surface, has a double pupil arranged so that the animal can see in water and air at the same time, the retina being divided on the median line to correspond to the double pupils.

Sight is usually absent in forms living in darkness, but some vestiges of the eye remain, such as parts of the lens, nerves, or retina. The eye of the mole, although buried under the skin, still remains as a fairly perfect eye. Blind forms occur in all classes except birds.

Parietal Eye

A vestigial parietal eye appears in many vertebrates and indicates that primitive vertebrates or their ancestors possessed a functional eye located in the center of the top of their heads. Many fossil skulls of placoderms and other early fishes show a foramen for such an eye between the parietal bones. Numerous fossil amphibians have a large parietal foramen, and it is present in the skulls of many modern reptiles as may be seen in the horned toad. *Sphenodon* has the best-developed parietal eye (Fig. 310) of any living vertebrate. It has a retina and a lens and is connected by nerve fibers to the brain, but it is covered by thick skin and does not function as a light-perceptive organ. The light-perceptive cells of the retina are directed toward the light whereas those of the functional eyes are directed away from the light.

The vestiges of a parietal eye present in the epiphyseal structures of most vertebrates indicate that only the distal part of the anterior structure develops into a median eye, the distal part of the posterior structure becoming a pineal body of endocrine function. Man has only a pineal body which has no nerve connections with the brain. The pineal apparatus associated with the parietal eye has been assumed to indicate that there was originally a pair of small eyes instead of a single median eye. Both of the epiphyseal structures of the cyclostomes show vestiges of an eye, indicating that these lowest of living vertebrates descended from an Agnatha ancestor which probably had

more than one parietal eye. Although the pineal structure and the parietal structure each bearing a vestigial eye are arranged in tandem when they appear together in the cyclostomes they arise embryologically as paired structures, and their nerve tracts (described on page 390) come from opposite sides of the brain. The question of when and where these eyes appeared and whether they were functional, has long been one of the intriguing problems of anatomy.

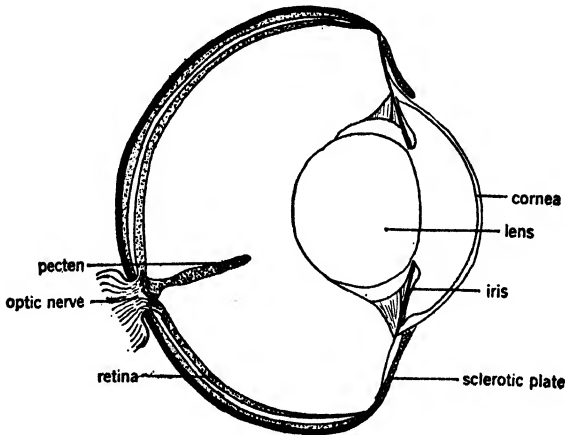


FIG. 357. Eye of lizard, diagrammatic. After Rochon-Davidneaud.

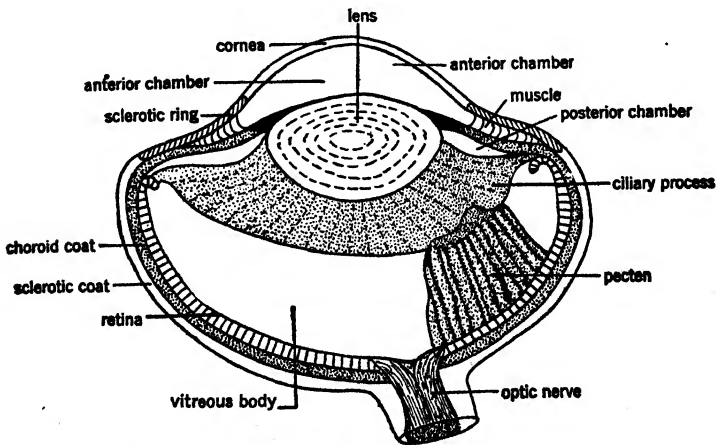


FIG. 358. Diagrammatic, sagittal section of eye of chicken.

The Eye of Various Vertebrates

Fishes

The eyes of fishes are well developed but are not readily adjustable for distant vision, which is not needed in the water because of turbidity. Consequently the lens is spherical and can be focused only by shifting

back and forth. Movable eyelids are not present, and tear glands are absent.

Amphibians

The eyes show a few changes necessary to land life, in the development of the lids, a better means of focusing the lens, and the development of the glands that aid in keeping the cornea moist. The lens is still round as in the fishes.

Reptiles

The eye (Fig. 357) usually has a well-developed third eyelid, the nictitating membrane, in addition to the usual pair of lids. Lacrimal and Harderian glands are present in land forms. Sight appears to be keen, and the power of focusing by changing the shape of the lens is greatly improved over amphibian conditions. The retina contains mostly cones with very few rods. Sclerotic bones often surround the eyeball.

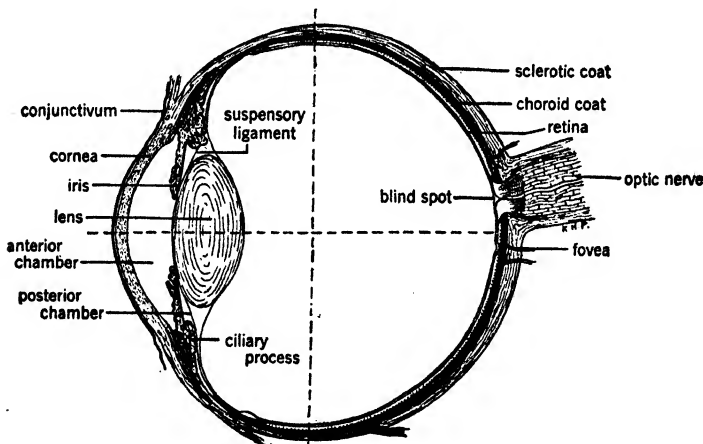


FIG. 359. Diagrammatic section of human eye. Redrawn from Plate and Luciana.

Birds

The eyes of birds are extremely keen, since it is upon them that the birds depend for food and safety. The eye of the chicken is fairly typical. The sclerotic coat is ossified, forming a series of sclerotic bones that surround the pupil. Hawks and owls have the sclerotic bones formed into a cup. The lens is held in place by the ciliary process, which is attached to the eyeball at the ora serrata. The iris, with its circular muscles, is stretched anterior to the lens and attached to the choroid. The posterior region of the eyeball is large and has a distinctive pecten (Fig. 358) developed at the point of entrance of the

optic nerve. The pecten extends toward the lens and is in contact with the ciliary process. The accommodation of the eye is obtained by the muscles of the iris and ciliary process, which lie between the cornea and the sclerotic coat. These muscles pull on the lens and change its convexity.

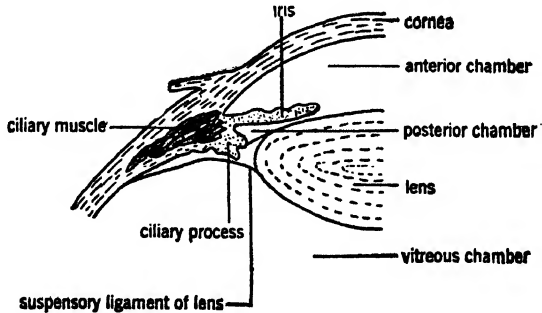


FIG. 360. Ciliary process and accessory structures of mammalian eye.
After Morris.

Mammals

The eye (Fig. 359) of the mammal is slightly different from that of reptiles and birds, since there is no pecten, no sclerotic bones, and only a vestigial nictitating membrane. The eyelashes are protective structures, at the bases of which the Meibomian glands supply an oily secretion to the lacrimal fluid. The lacrimal glands, on the outer border of the eyes, supply the lacrimal fluid for lubrication.

CHAPTER SEVENTEEN

Endocrine Glands

The endocrine structures consist of a number of glandular bodies that play a very important part in the lives of all vertebrates, from the first developmental stages to death. Though not clearly recognized as yet, it is probable that similar functions are performed by some substances in the invertebrates. It has been shown recently that plants have materials comparable to the hormones of animals. The hormones are chemical substances that are formed in the endocrine glands and distributed through the blood stream; for this reason the endocrine glands are called ductless glands. For the most part, the endocrine glands are small bodies, although some may have quite an appreciable mass of material; and although some of them have ducts, these ducts are not connected with the endocrine system. The action of these materials is quite rapid, and one of the features of a hormone is the extremely small quantity necessary to accomplish results. The endocrines exercise a control over the body somewhat comparable to the action of the nervous system, but in a different way, since the endocrine control is chemical. They appear to be responsible for correlating growth, both in initiating and in stopping it; for correlating the processes of metabolism; and for establishing a system to maintain the relations between the different body tissues. Although these glands appear to have certain definite functions, they also tend to affect one another; if one gets too active, it is checked by the action of another gland. They are specific not only for the animal from which they have been taken but for other animals as well, since glandular extracts of one group seem to have similar effects on animals of an entirely different class. Knowledge of the action of the glands is obtained by several types of experiments, such as removal of the glands, introduction of the extracts, grafting of glands, and a wide range of these procedures. —

Although most of the knowledge of the endocrines has been developed since 1900, it is certain that some of the structures, and even their actions, have been known for centuries. Since castration in both man and animals has been practiced for a long period of time, it is probable that the effects of this operation were among the first to be known

and recognized. The old custom of eating adversaries to gain their strength and valor may have had its origin in the belief that there was a transfer of these qualities via the digestive tract. The idea of eating parts of animals as cures for illness in corresponding organs has had a prominent place in medical lore and even today has followers. Eating brains, livers, lungs, and gonads is an old practice. From the Greeks to comparatively modern times, there has been some knowledge of the glands and something of glandular action, but the real knowledge had to wait for the developments of the comparative anatomists, the experimental physiologists, and zoölogists, the microscope, and the findings of chemistry.

In contrast to the rather hazy ideas of the ancients, the first real work on endocrines was done by Johannes Müller, who wrote on internal secretions as early as 1833. Bertold, in 1849, transplanted testes in capons and commented on the results. Brown-Sequard worked on organ therapy and performed some experiments on the secretions of the gonads. The name "hormone" was coined by Bayliss and Starling in 1906, when they made the discovery of secretin from the duodenum. They considered these materials as "chemical messengers." Since then the interest has increased, until now endocrinology has a very important place among the experimental sciences. The medical profession makes extensive use of the endocrine materials, and a number of them, such as thyroxin, pituitrin, epinephrin, cortin, testosterone, and estrone, are available. Some of these have been prepared synthetically, but they are usually prepared from the glands of some animal that is readily available and can furnish a large supply.

The principal endocrine structures consist of two in the head region, the pineal and the pituitary; four in the neck, the thymus, thyroid, parathyroids, and ultimobranchials; at least three in the body cavity, the pancreas, adrenals, and the gonads. It is possible that others will be discovered as the knowledge of their action and structure increases (Fig. 361).

Pineal

The pineal structure, or epiphysis, is a small outpouching from the roof of the diencephalon, the second division of the brain (Figs. 310, 322, 325, 361). It is found in most vertebrates but is sometimes degenerate. In the elasmobranchs, the pineal structure reaches the roof of the skull where there is often a foramen for this gland. It is apparently absent in *Myxine* and in crocodiles. In mammals it appears as a pinkish pouch that is covered by an overgrowth of the cerebral lobes, and it is much more gland-like than in the lower animals. The nerve supply comes from the brain and the autonomic system. The

status of this as an endocrine has been doubted, although, when disturbed by tumors or other abnormalities, there may be an acceleration of growth, precocious development of the mentality, and premature sex development. Experimental evidence has been rather contradictory but is becoming more positive. In humans, the pineal body is glandular in early life but, after puberty, decreases in size, and the glandular tissue is replaced by fibrous tissue. White rats in which the pineal had been removed for a number of generations showed definite effects that place the pineal in a different light. In these experimental animals, the number of litters was increased, but the size of the young and their subsequent growth were retarded. Later generations matured sexually in about half the number of days, but the size was considerably less than that of the normal animals. A definite retardation of growth appeared to be caused by the removal of the pineal in these experiments.

Pituitary

The pituitary gland is on the lower side of the diencephalon and appears to be a structure present in all vertebrates and probably in the protochordates. The pituitary is one of the oldest of the known endocrines, since its written history starts with Aristotle, Galen, and the early anatomists. Its embryology was first made known by Rathke (1838), who showed that it was formed by an outpouching from the brain that extended out from the floor of the diencephalon, and a corresponding inpouching from the roof of the mouth, the Rathke's pocket of anatomy. These two structures come together so that the Rathke's pocket extends anteriorly, forming the anterior lobe, while the infundibular pouch from the diencephalon extends posteriorly, forming the posterior lobe. Little of its function was known until early in the eighteenth century, when it was associated with certain abnormalities that occur in man—acromegaly, gigantism, and

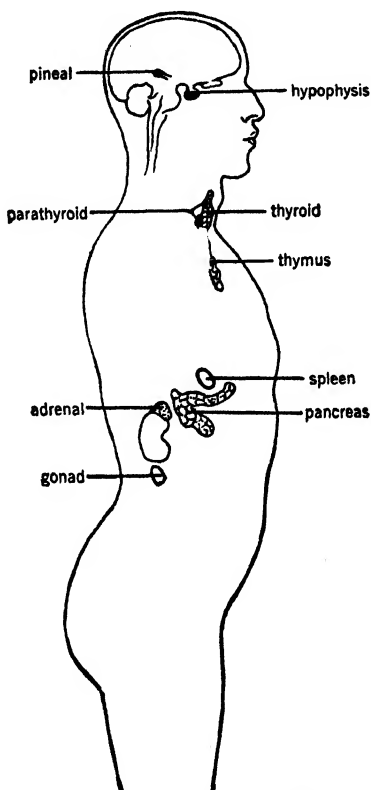


FIG. 361. Diagram showing the location of the more important endocrine glands of man.

dwarfism. Acromegaly is the result of a hyperactivity of the gland in the adult, causing certain parts of the skeleton to grow in a most startling manner until finally normal proportions are lost. Giantism is also the result of hyperpituitarism in the young animal, and, though growth may extend far beyond normal, the animal remains proportional and normal in features other than size. Dwarfism results from the hyposecretion of the anterior lobe in the young animal, and here again the reduction in size is proportional, so that the end result is an individual much dwarfed but with all parts of the body in proportion, the midgets so familiar in the sideshow and circus. At least six well-known hormones are secreted by the anterior lobe.

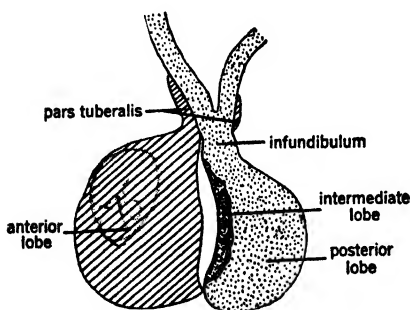


FIG. 362. Sagittal section of human hypophysis. After Morris.

Early in the study of the gland, it was recognized that the anterior gland was quite different from the posterior in action, and that the removal of the anterior gland usually caused death. Now, however, it is understood that the probable cause of death is not the removal of the gland but injury to the brain in the region of the tuber cinereum.

The posterior lobe is known to secrete two hormones. The importance of the pituitary has increased with a more thorough understanding of its many functions, and it is now considered a kind of master gland, since among its important functions is included control over some of the other endocrine structures and their secretions.

The pituitary is well established in the cyclostomes, but there is a peculiar relation to the hypophyseal sac, which opens into the narial passage and also to the pharynx. From fishes to man, the pituitary is always a prominent structure on the ventral side of the diencephalon (Figs. 316, 318, 322, 327). Anatomically, the pituitary consists of four parts (Fig. 362) the anterior lobe, pars tuberalis, pars intermedia, and the posterior lobe. The infundibulum carries its lumen with it, extends posteriorly, and becomes glandular at the posterior end, thus forming the posterior lobe. Part of the infundibulum may become much folded, thus forming the saccus vasculosus of the shark and other fishes. The pocket of Rathke pushes dorsally and anteriorly, also carrying its lumen with it, and comes to lie between the infundibulum and the brain case. The intermediate lobe, pars intermedia, is between the anterior and posterior lobes, varying in size from a very distinct section to a very small region and sometimes appearing to be missing entirely. The pars tuberalis is a portion of the gland that develops at the base

of the infundibulum, partly surrounding it, and in very close association with the brain. Both the intermediate lobe and the pars tuberalis are considered parts of Rathke's pocket. The color of the pituitary is quite different from that of the brain, and the gland is of sufficient size so that it is unmistakable even in small vertebrates. In many of the higher animals the pituitary is so surrounded by the sella turcica that it remains with the skull when the brain is lifted from the brain case. In lower animals the pituitary is easily reached through the roof of the mouth, but in the higher animals the easiest approach is through the nose and the roof of the nasal passage or through the side of the skull. Since experimental removal may injure parts of the brain, especially in the region of the tuber cinereum, much discretion must be exercised in interpreting the results of removal. The removal of the anterior lobe seems to show that it is associated with growth development, maturation, and proper function of the gonads, the mammary glands, thyroid glands, growth hormones, and adrenal functions. The posterior lobe alone affects respiration, raises arterial pressure, stimulates uterine contractions, stimulates the digestive system, and has some relation to pigmentation. The intermediate lobe also has some relation to the distribution of pigment granules in pigment cells.

The removal of the whole gland, if this is possible without injury to the brain, has a very decided effect on the body of the animal. Since the operation has been carried out on all classes of animals, the results are quite well known in all the groups. The most striking effects are the disturbances of the other endocrine glands and their functions. The effects on the secondary sex characters, caused by the removal of the anterior lobe of the pituitary in young animals, are quite similar to those caused by the removal of the gonads. In males, there is the same reduction of the size of the secondary sex structures, and the gonads themselves become very small. Similar changes occur in females; the ovaries and their secondary sex structures fail to reach normal size, remaining infantile and undeveloped. Materials that react upon the ovaries have been discovered in the urine of pregnant females, placenta, amniotic fluids, and blood. These hormones, called FSH and LH, have been isolated and their effects studied. FSH, the follicle-stimulating hormone, acts on the ovary; LH, the luteinizing hormone, stimulates the formation of the corpus luteum.

Thymus

The thymus gland, known as the throat sweetbread of the butcher shop, is located on the ventral surface of the trachea and is a gland of young animals, since it is very large during the growing periods and shrinks materially as the animal approaches and reaches maturity.

(Fig. 363). It is more closely related to the lymphatic system than to the endocrines, containing lymphocytes along with typical thymic cells. It also contains nucleoplasm in large quantities and must be of value to growing animals. Disturbances in the lymphatic system are often associated with abnormalities or diseased conditions of the thymus, and it appears to have some relation to the growth of the skeleton, gonads, and nutrition, although its status as an endocrine has been somewhat questionable. The removal of the pituitary has a decided effect on the thymus.

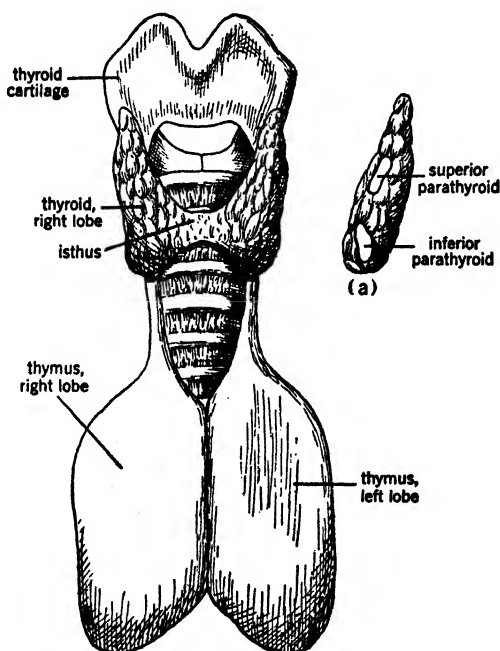


FIG. 363. Anterior aspect of the human larynx and trachea at birth, to show the thyroid and thymus, in relation to these structures. (a) Dorsal aspect of a lobe of thyroid to show the parathyroids. (Redrawn from Morris' *Anatomy*.)

The thymus consists of paired glands that take their origin from the epithelium of the dorsal angles of the gill pouches. The actual origin is quite variable, and, though the lower forms have them originating from all the gill pouches, in higher animals their origin is more restricted and usually from the third and fourth gill pouches only. It is probable that the gland is present in the cyclostomes, but it is rather difficult to demonstrate with certainty; in the gnathostomes, however, it is universal in its distribution. In fishes, the thymus consists of a number of glands in a series, along the dorsal angles of the gill pouches. In frogs, the glands are posterior to the jaw and at the posterior, ventral

border of the tympanic annulus; in urodeles, they are posterior to the gills. In birds and reptiles, the glands lie along the neck and are associated with the internal carotids, usually being ventral to these vessels. In mammals the thymus extends anteriorly as far as the thyroids, and the posterior end may extend to the base of the heart in young animals.

Thyroids

The thyroids once thought to be descendants of the endostyle of the protochordates, are present in all vertebrates (Figs. 363, 364). Originally the thyroids had a duct, which is now lost, and the secretions must be taken up by the blood stream. The thyroid is unpaired in fishes; scattered along the branchial arches in the amphibians; unpaired in reptiles; paired in birds and usually at the base of the bronchi; and in mammals it is usually paired and may have a connecting bridge, a condition present in most placental mammals. Whereas the thyroids in the lower vertebrates may be located in different positions along the branchial bars, in mammals they are close to the pharynx and trachea. In abnormal conditions, where the thyroid is enlarged, it may become quite conspicuous in the human, and for this reason it has probably been known for a long time. It is recorded that the Chinese, 150 B.C., recognized the condition and used iodine for a cure.

The thyroids have a distinctive structure, with numerous vesicular cells that secrete a colloid substance containing iodine. In man, the thyroids are quite large, reddish brown bodies that are ventral to the larynx and along the sides of the trachea. There is a large blood and nerve supply. The thyroid is one of the most active of the endocrines, and the results of either hyper- or hyposecretion are quickly apparent in man and animals. The two conditions, however, produce very different effects. Hypothyroidism, or too little of the secretion, causes in young animals a condition called cretinism. The affected individuals remain infantile and never grow up either mentally or physically, since the whole body growth is retarded, including the brain and mentality, and the metabolism is seriously disturbed. Feeding extracts of the gland to young animals in which the supply is deficient relieves the condition to some extent, and there may be an approach to normality. When the adult lacks the thyroid secretion, a number of body conditions appear, such as a swelling of the skin, lowered metabolism, and disturbances in the circulatory and nervous systems, a condition known as myxedema. Hyperthyroidism, in which there is too much of the secretion, causes an increased activity as though all the body processes were geared up to an impossible pace, so that the whole body tends to burn out. Because of its accessibility, there has been much experi-

mentation on the thyroid, and it is perhaps as well understood as any of the endocrine glands. There is a very interesting connection between the thyroid and the pituitary, the thyroid being seriously affected when the pituitary is removed.

Parathyroids

The parathyroids are known in all vertebrates except the fishes, and it is probable that they are represented in this group by some of the epithelial bodies (Figs. 363, 364). Remak discovered them in 1885, but their functions were not known until much later. In 1880, Ivar

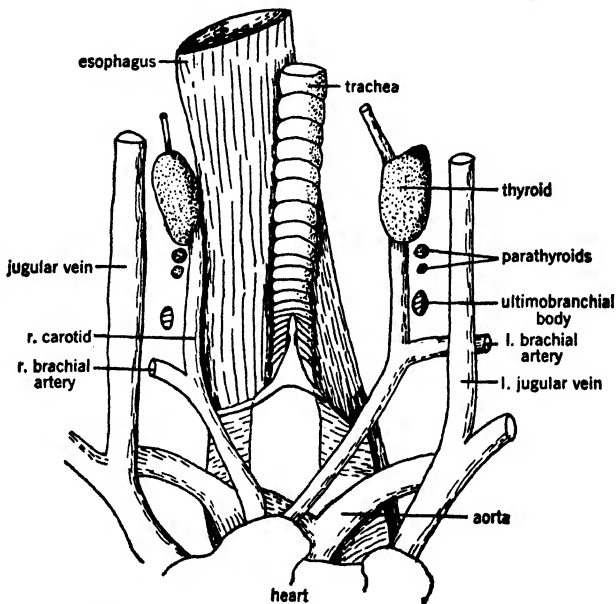


FIG. 364. Blood vessels in the region of the heart in the domestic chicken, to show associated endocrine glands.

Standström worked on the parathyroids and decided that they were undeveloped thyroids. E. Gley, in 1882, found out that their removal caused death through tetany. They came into real prominence through the work of Kohn (1895), who made a thorough study of their anatomy and histology. Much of the information regarding the parathyroids came through a study of the thyroids.

These small bodies developed from the third and fourth gill pouches in man; they are usually four in number and about the size of a bean. They may be on the surface or imbedded in the substance of the thyroid, a circumstance that has led to much confusion and to dissimilar results in experimental work, since in some animals they would be removed

with the thyroids, but in others the thyroid operation would not destroy them. With a lack of knowledge of the position of the parathyroids, it was difficult to explain why some animals always died after the removal of the thyroids and others lived. Although the parathyroids have not been found in fishes, it is probable that they exist in some form, since the regulation of the calcium supply to the skeleton and to other parts is their function. The first definite bodies that can be classified with certainty appear in the Amphibia, where they resemble small epithelial bodies. They are mesial to the external jugulars in toads and frogs, and are paired on each side, four in all. Urodeles have a similar pair on each side, just posterior to the external jugular. They are present in all reptiles, being located slightly posterior to the thyroids and more lateral, along the side of the neck, appearing as small oblong bodies usually consisting of two pairs. In snakes, they are closer to the skull than in other reptiles. In birds the parathyroids are usually close to the thyroid and between the jugulars and the carotids, but a few have them on the surface of the thyroid. They may be single or paired, and they have the characteristic yellowish color. In mammals they consist of two or three pairs and are always in association with the thyroids, being either on their surface or imbedded in their material.

The structure is rather simple, since they consist mainly of a mass of epithelial cells showing some strand and trabecular arrangement and having colloid between the cells. The function of the parathyroid is the regulation of the calcium content of the blood and the prevention of the formation of certain substances such as guanidine which appears in the blood after their removal. Their removal results in death in a short time through a disturbance of the calcium metabolism, causing a typical tetany.

Pancreas

The pancreas, a structure present in all vertebrates, is assumed also to exist in the protochordates, perhaps in the walls of the intestine. The pancreas develops as an outpouching from the digestive tract just opposite the diverticulum forming the liver and in adult animals is usually found in a fold of the intestine just posterior to the duodenum. Its importance as a digestive gland is well known, but it was not suspected of other activities until the discovery of Langerhans (1869) attracted attention to the interstitial cells, now called the "Islets of Langerhans." The investigations of Banting, Best, and others, in 1921, showed the presence of a hormone named insulin in the pancreas, which is concerned with the regulation of the sugar content of the blood so that a proper sugar metabolism is maintained—a feature

very important to all vertebrates. The various distressing metabolic changes, and the loss of sugar through the urine, a diabetic condition, are now very well controlled by the administration of insulin at regular intervals. The medical supply of the hormone is obtained from the pancreas of some of the large domestic animals commonly slaughtered for food and hence available in large quantities (Figs. 210, 218).

Adrenals

The adrenals or suprarenals are a pair of glands so named because of their position, which is usually close to the kidneys. (See p. 358.) In the higher vertebrates each gland consists of an outer cortex and an inner medulla, which have different origins and different functions. The cortex is derived from the same group of mesodermal cells that form the kidney; the medulla is derived from the chromaffin cells, the same material used in the formation of the sympathetic system. The two parts are separate in fishes and amphibians and because of their position between the kidneys are called interrenals. In reptiles the two parts are closely associated; in mammals, they are enclosed in a single capsule, usually at the dorsal apex or slightly mesial to the kidney (Figs. 300, 301).

The adrenals have had a long history, since they were discovered by Eustachius in 1563. They excited little comment or curiosity, however, until Thomas Addison, in 1885, discovered Addison's disease, and associated it with a disorder of the adrenal gland. The medulla produces the hormone, epinephrin (adrenalin), which was isolated by Abel in 1900. The cortex produces a hormone, cortin, which was isolated by a number of workers in the years 1929-30.

In mammals the gland is somewhat triangular, usually forming a cap on the anterior, mesial region of the kidney. The outer layer or cortex is lighter in color than the inner layer or medulla. The removal of the cortex causes death, but the removal of the medulla is not so serious. The epinephrin produced by the medulla stimulates the sympathetic system, speeds up the heart, and increases the blood sugar. When the cortex is removed, the results are disturbances in digestion, kidney action, sugar distribution, and other physiological activities. Although the function of cortin is not well understood, it plays a part in the development of sex. An excess of cortin causes precocious sexual development in the male and the development of secondary male sex characters in the adult female. The isolated hormone, cortin, is able to keep adrenalectomized animals alive for long periods of time and perhaps indefinitely.

Gonads

Since historic times it has been recognized that the gonads have a decided influence on the body form. Castration has long been practiced, both on domestic animals and man, and its effects were well known, since the secondary sexual characteristics did not appear in animals castrated at an early age. Castration of adult animals causes much less change in the animal body. The obvious differences between bulls and steers, roosters and capons, eunuchs and normal men gave concrete evidence of the relationships of the gonads to the secondary sex characteristics. There is some question of the actual function of the interstitial cells of the testes, but it is certain that the testes do contain materials that will modify the effects of castration if transplanted into the castrated animal. The interstitial cells appear to have some relation to the development of the secondary sex characters. A well-known manifestation of the hormone action appears in twin calves, male and female, where hormones of the male so influence the development of the female before birth that the female is abnormal, having incomplete sexual organs and being sterile. The condition of this animal, known as the freemartin, appears to be a direct result of the action of a hormone from one sex, inhibiting the development of the opposite sex.

Ovaries

The gonads of the female carry certain endocrines that are essential to the normal development and physiological functioning of the sex. The removal of the ovaries causes a series of effects that can be changed back to normal if ovaries are grafted back into the body. Male gonads, when grafted in the body of a female, are likely to cause an approach to the male form, particularly the secondary sex characteristics. The pituitary, again, has a decided influence on the female gonads. The product of the Graafian follicle, estrone (theelin), has been isolated not only from the follicles of the ovary but also from the liquor of the follicles, the urine, the amniotic fluid, and other reproductive structures. Progesterin or corporin is elaborated from the modified follicular cells after ovulation. The action of this hormone is concerned in the events that follow the initial preparation of the reproductive organs for the reception of the egg and the ensuing gestation, decidua formation, and probably other functions. Estrone is concerned primarily in the characteristic changes that occur in the uterine tract, the vagina, and in the behavior associated with the occurrence of estrus. The origin of these gonadal hormones is not clear; although they seem to be related to the gonads and most of them occur in the gonads,

they also are found in other parts of the body and even in the opposite sex. Theelin is present in the urine of males.

Testes

Male hormones are known from the higher vertebrates, and two have been isolated: androsterone from male and also from female urine, and from the male testis and blood; testosterone from the testis. These stimulate the development of secondary male characters such as spurs, combs, and hair. When injected into females they inhibit ovulation. Both are found in females as well as males, and the sex apparently determines which will predominate. The origin of the male endocrines or hormones is not clear, but the testes seem to be related to their production in the males, as their removal in early life results in underdevelopment of the secondary sexual characters.

Duodenum and Secretin

The first endocrine substance to be described resulted from the discovery of secretin by Bayliss and Starling in 1906, when they isolated secretin from the duodenum. They proved that some substance from the duodenum, carried by the blood stream to the pancreas, initiated the flow of the pancreatic juice. From this initial discovery has grown the general idea of the action of hormones, which often influences parts of the body far removed from the gland and the place of manufacture. A second hormone from the duodenum causes the gall bladder to discharge its contents. This product, cholecystokinin, is probably one of several correlating the activities of the different parts of the digestive system.

Ultimobranchial Bodies

The gill pouches are the source of a number of small bodies that have an endocrine function. The ultimobranchial structures are small glands that originate from the fifth pair of gill pouches (Fig. 364). In man they are closely associated with the thyroids and apparently disappear as definite structures. Their history in the lower animals, where they are retained as definite glands, can be followed through from fishes to mammals. They appear as small epithelial bodies posterior to the thyroids, and they have colloidal cells that suggest a similarity to other glands from this same source.

Our knowledge has reached only the threshold of internal secretions. All tissues probably secrete various substances of an endocrine nature

into the blood. The processes of nerve cells seem to secrete minute quantities of an endocrine nature during excitation. The liver actually has several internal secretions, although these are not all strictly endocrine in function. The liver secretes urea and dextrose into the blood and also substances which probably function as endocrines.

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Glossary

- ABDUCENS.** The sixth cranial nerve.
- ABDUCTION.** The withdrawal of a part from the median axis of the body.
- ABDUCTOR.** A muscle that pulls a limb or part away from the median axis of the body.
- ABOMASUM.** The fourth division of a ruminant stomach.
- ACETABULUM.** The socket in the pelvis for the articulation of the head of the femur.
- ACINOSE.** Shaped like a cluster of grapes.
- ACRANIA.** Applied to chordates lacking a brain case (protochordates, *Amphioxus*).
- ACRODONT.** Pertaining to teeth ankylosed to the edge of the jaws.
- ACROMEGALY.** An abnormal enlargement of the bones of the skull, thorax, and limbs, caused by a diseased pituitary gland.
- ACROMION PROCESS.** A ventral prolongation of the spine of the scapula.
- ACTINOSTS.** Radial, distal elements of a fish fin.
- ADDUCTION.** The movement of a part towards the median axis.
- ADDUCTOR.** A muscle that pulls a limb or other structure towards the median axis.
- ADDUCTOR ARCUUS BRANCHIALES.** Small adductors of the gill arches.
- ADDUCTOR LONGUS and BREVIS.** Adductors of the thigh.
- ADENOID TISSUE.** Lymphatic or gland-like tissue. (Upper part of pharynx.)
- ADRENAL GLAND.** An endocrine gland, usually near the kidney.
- AFFERENT.** Passing or conducting to a structure, as afferent arteries to gills, afferent nerve fibers to brain, etc.
- AGNATHA.** A term applied to jawless vertebrates (cyclostomes).
- AIRSAC.** Respiratory bladder accessory to the lungs in reptiles and birds.
- ALBINO.** White, lacking pigment.
- ALISPHENOID.** A chondral skull element, on the sidewall of the brain case.
- ALLANTOIS.** An embryonic membrane in reptiles, birds, and mammals.
- ALVEOLATED.** With small cavities.
- ALVEOLUS.** Small pits in lungs, where the exchange of gases occurs.
- AMMOCOETES.** Larval stage of a lamprey.
- AMNION.** A thin, embryonic membrane, filled with a liquid, which encloses the embryos of reptiles, birds, and mammals.
- AMNIOTE.** A term including all vertebrates that have an amnion during embryonic development (reptiles, birds, and mammals).
- AMPHIARTHROSIS.** Flexible, but not freely movable, joint between bones.
- AMPHICOELOUS.** Referring to a type of vertebra in which both ends of the centrum are concave.
- AMPHIPLATYAN.** Referring to a type of vertebra in which both ends of the centrum are flat.
- AMPHISTYLIC.** Designating the method of attachment of the upper jaw to the skull, by a process on the palatoquadrate, and also by the hyomandibula.
- AMPULLA.** A small, flask-shaped cavity.
- AMYLOPSIN.** A starch-splitting enzyme of the pancreas.
- ANABOLISM.** Constructive chemical processes concerned in building up protoplasm and cells.

- ANAPSID.** Skull having no temporal openings or arcades.
- ANGULAR.** A dermal bone of the mandible.
- ANKYLOSIS.** The joining of two or more bones or hard parts to form a single structure.
- ANNULAR RINGS.** Concentric markings on fish scales, developed by new growth, after the winter months.
- ANTERIOR.** Toward the head end.
- ANUS.** The posterior opening of the alimentary canal.
- AORTIC ARCHES.** Primitively, a series of six pairs of arteries, running through the branchial arches and connecting the ventral aorta with the dorsal aorta.
- APONEUROSIS.** Sheets of fascia which cover and form attachments for muscles.
- APTERIA.** The area between feather tracts.
- AQUEOUS HUMOR.** A refracting fluid between the lens and the cornea of the eye.
- ARACHNOID LAYER.** The thin membrane interposed between the outer dura mater and the inner pia mater, of the brain and cord coverings.
- ARBOR VITAE.** A term applied to the nerve tracts of the cerebellum because of the pattern that they form. Also called the "Tree of Life."
- ARCADE.** An arch of bone surrounding the temporal fossa of the skull, in some reptiles.
- ARCHENCEPHALON.** The primitive forebrain.
- ARCHINEPHROS.** Primitive kidney extending the entire length of body cavity.
- ARCUALIA.** Paired cartilages formed in sclerotomes, about notochord and nerve cord, and giving rise to vertebrae.
- ARTICULAR.** The ossified end of the Meckelian cartilage of the mandible.
- ARYTENIDS.** Paired cartilages of the larynx.
- ASTEREOSPONDYLOUS.** Pertaining to shark vertebrae, in which the calcifications of the centrum occur in radiating plates.
- ASTRAGALUS.** A bone of the proximal row of the tarsus.
- ATLAS.** The first neck vertebra.
- ATRIAL PORE.** An opening near the anus of *Amphioxus*, which leads from the chamber enclosing the gills, to the outside.
- ATRIOVENTRICULAR BUNDLE.** A muscular bundle containing nerves, that transmits the atrial rhythm to the ventricle. A timing bundle.
- ATRIUM.** A chamber; atrium of heart, lungs, nose, etc.
- AUDITORY BULLA.** A thin-walled bulb formed by the tympanic bone.
- AUDITORY MEATUS, EXTERNAL.** The exterior opening of the ear. A passage leading from the tympanic membrane to the outside.
- AUDITORY MEATUS, INTERNAL.** The opening on the inner side of the petrosal bone which transmits the auditory and other nerves.
- AUDITORY TUBE.** The passage leading from the middle ear to the pharynx.
- AURICLE.** Major receiving chambers of heart, properly applied to divided parts of atrium.
- AUTONOMIC NERVOUS SYSTEM.** A specialized part of the peripheral system, consisting of nerves and ganglia, that is concerned in involuntary actions and processes.
- AUTOSTYLIC.** Designating the method by which the upper jaw is attached to the cranium, by a process from the palatoquadrate, the hyomandibula taking no part.
- AXILLA.** The armpit.
- AXINOST.** The basal elements of median fins in contact with or close to the neural spines of the vertebral column. Also called interspinals.

AXIS. The second vertebra of the neck. Also called epistropheus.

AXON. A process which leads nerve impulses away from the neuron.

AZYGOUS. Unpaired.

BARB. A thread-like part of a feather extending out from the shaft.

BARBEL. Tentacle-like structure on the heads of many fishes.

BARBICEL. A small process on the barbule of a feather.

BARBULE. One of the small hooks fringing the barbs of a feather.

BASALIA. The proximal elements at the base of a cartilaginous fin.

BASEOST. The basal region of median fin-rays, distal to the axinosts.

BASIBRANCHIAL. The ventral element of the branchial or gill arches.

BASICRANIAL REGION. The ventral region of the skull.

BASIDORSALIA. A part of a sclerotome concerned in the formation of a vertebra.

BASIHyal. The basal element of the hyoid arch.

BASILAR MEMBRANE. Membrane in cochlea of inner ear, forming floor of scala media.

BASILINGULAR PLATE. Main body of the hyoid cartilage.

BASIOCCIPITAL. A chondral bone, forming the base of the occipital region of the skull.

BASIVENTRALIA. A part of a sclerotome concerned in the formation of a vertebra.

BELL'S LAW. The law of distribution of the nerve fibers in the dorsal and ventral roots of a spinal nerve. The ventral root carries nothing but motor fibers; the dorsal root is mainly sensory.

BICEPS. A large flexor of the arm at the elbow.

BICIPITAL. Two-headed; e.g., some ribs.

BICUSPID. A tooth with two cusps. A valve between the left atrium and left ventricle.

BILATERAL. A type of symmetry in which the median plane divides the body into two practically equal parts, which are mirror images of each other.

BLASTOMERE. One of the cells formed in the primary divisions of an egg.

BLASTOPORE. The opening in a gastrula that leads to the archenteron.

BOWMAN'S CAPSULE. A double-walled, cup-like vesicle of the excreting unit of the kidney, into which the blood vessels extend to form a glomerulus.

BRACHIAL. Major structures of anterior paired appendages or limbs.

BRACHIUM CONJUNCTIVUM. A tract of nerve fibers extending from the cerebellum to the mesencephalon.

BRACHIUM PONTIS. A transverse band of nerve fibers, passing under the brain stem and connecting the two cerebellar lobes.

BRACHYDONT. Descriptive of molar teeth having low crowns; e.g., those of a cow.

BRANCHIAL. Structures of the gills or visceral skeleton.

BRANCHIAL BASKET. The visceral skeleton of the cyclostomes.

BRANCHIOSTEGAL RAYS. The ventral series of dermal bones protecting the gills in fishes.

BROAD LIGAMENT. Folds of the peritoneum holding the ovary in place.

BRONCHIOLES. Small tubes in the lungs, which terminate the bronchi.

BRONCHUS. One of the tubes connecting the trachea with the lungs.

BUCCAL. Pertaining to mouth or mouth cavity.

BULBUS. A muscular enlargement at the base of the aorta; e.g., in fishes and amphibians.

BUNDLE OF HIS. A neuromuscular bundle of the heart. A timing bundle.

BUNODONT. Descriptive of molar teeth having several rounded cusps.

BURSA. A sac-like cavity.

BURSA FABRICII. A glandular pouch that opens off on the dorsal side of the cloaca in young birds. Atrophies in the adult.

CAECUM. A blind pouch or diverticulum; e.g., such as vermiform appendix.

CALCANEUM. Large proximal bone in tarsus (heel bone).

CANALICULUS. A minute canal in bone connecting the Haversian canals.

CANINE TEETH. Single, pointed teeth, just posterior to the incisors.

CAPILLARIES. Minute, thin-walled tubules connecting blood vessels.

CAPITATE (CARPALE 3). A bone of the distal carpal row, at the base of the third metacarpal.

CAPITULAR HEAD (RIB). The primary head of a bicapital rib.

CARDIAC. Structures related to the heart.

CARDINALS, ANTERIOR. Paired vessels returning the blood from the head region in fishes and amphibians.

CARDINALS, POSTERIOR. Paired vessels returning the blood from the body region in fishes and amphibians.

CARINATE. Birds in which the sternum is keeled. Usually fliers.

CARNIVOROUS. Feeding principally on flesh.

CARPALIA. Distal series of bones of carpus.

CARPALS. The series of bones in the wrist or carpus.

CARPUS. Wrist.

CARTILAGE (GRISTLE). Elastic material usually associated with skeleton.

CASTRATION. The removal of the testes.

CELIAC AXIS. Major unpaired artery from aorta to stomach, spleen, and intestine.

CELIAC PLEXUS (SOLAR PLEXUS). A network of nerves and ganglia forming a plexus posterior to the stomach.

CENTRALIA. Small bones representing a median row in the carpus or tarsus. Sometimes but not always present.

CENTRUM. The body of a vertebra.

CEPHALIC. Pertaining to the head.

CERATOBANCHIAL. An element of the branchial arch.

CERATOHYAL. An element of the hyoid arch.

CERATOTRICHIA. The horny, dermal fin-rays of sharks.

CEREBELLUM. A supra-segmental structure on the dorsal side of the metencephalon, associated with coordination.

CEREBRAL COMMISSURE, INFERIOR. A tract of nerve fibers, connecting the median geniculates.

CEREBRUM. The two large hemispheres of the forebrain.

CERVIX. The neck, particularly the neck of the uterus.

CHEIROPTERYGIUM. Skeleton of the appendage of four-footed animals (tetrapods).

CHIASMA (OPTIC). A crossing of the optic nerves.

CHITIN. The skeletal material of arthropods.

CHOANA. A funnel-shaped opening.

CHOLECYSTOKININ. Hormone from the duodenum which causes the contraction of the gall bladder.

CHOLEDOCHAL DUCT. The common bile duct.

CHONDROCRANIUM. The cartilaginous neurocranium of embryos and low fishes.

CHORDA TYMPANI. The glossopalatine branch of the seventh cranial nerve, associated with the middle ear in higher vertebrates.

CHORDAE TENDINAE. The tendons of the heart valve muscles.

- CHORION.** An extra-embryonic membrane of amniotes.
- CHOROID COAT.** A vascular coat between the retina and the sclerotic coats of the eye.
- CHOROID PLEXUS.** The thin, richly vascular roof of the diencephalon and myelencephalon, which extends as folds into the ventricles of the brain.
- CHROMAFFIN CELLS.** Cells of the sympathetic ganglia that do not become neurons but form the beginning of the suprarenal gland.
- CHROMATOPHORES.** Pigment cells that change in shape and size, thus producing color changes.
- CHROMOSOMES.** Definite staining bodies in a cell, which reproduce themselves in cell division. In germ cells they bear hereditary characters.
- CILIA.** Hair-like processes, often present on cells.
- CILIARY INGESTION.** A method of directing food into the digestive tube by means of ciliated tracts; e.g., as in *Amphioxus*.
- CILIARY MUSCLE.** A muscle of the ciliary process of the eye, which assists in accommodation.
- CIRCUMDUCTION.** Movement of a limb so that the distal end describes a circle.
- CIRCUMVALLATE PAPILLAE.** Small papillae on the tongue.
- CLAUSTRUM.** The anterior Weberian ossicle.
- CLAVICLE.** A dermal bone of the pectoral girdle.
- CLEIDOMASTOID.** A muscle between the clavicle and the mastoid region of the skull.
- CLEITHRUM.** A large dermal element in the shoulder girdle of fishes and primitive amphibians.
- CLITORIS.** Erectile tissue of the female genitalia, the homologue of the penis.
- CLOACA.** The common cavity for the openings of the digestive and urogenital systems.
- COCHLEA.** The spirally coiled lagena of the mammalian inner ear.
- COELOM.** The body cavity of chordates.
- COLON.** A part of the large intestine.
- COLUMELLA AURIS.** A rod in the middle ear extending out from the stapedial plate to the tympanum. The tip is formed by the extra-stapedial cartilage.
- COLUMELLA CRANII.** A rod-like bone (epipterygoid) of the skull between the pterygoid and parietal of lacertilians.
- COMMISSURE.** A tract of fibers connecting similar parts on opposite sides of the brain or cord.
- COMMON CARDINALS.** Ducts of Cuvier or lateral vessels collecting blood from anterior and posterior cardinals, and emptying into sinus venosus.
- CONCRESCENCE THEORY.** Pertaining to the formation of mammalian molars by the growing together of single cones.
- CONDYLE.** A convex articular surface of a bone.
- CONJUNCTIVA.** The thin epithelial covering of the anterior face of the eye.
- CONTOUR FEATHERS.** The feathers forming the body covering.
- CONUS ARTERIOSUS.** A cone-shaped valved structure of the heart emptying into the aorta.
- COPRODAEUM.** The part of the cloaca into which the intestine discharges.
- CORACOBRACHIALIS.** A muscle of the shoulder that adducts the humerus and holds the head of the humerus in the glenoid cavity.
- CORACOID.** A bone or cartilage of the pectoral girdle.
- CORIUM.** The dermis, or deep layer of the skin containing blood vessels, nerves, muscles, pigment cells, etc.

- CORNEA.** The transparent part of the sclerotic coat covering the anterior face of the eye.
- CORNULATE CARTILAGES.** Small cartilages of the larynx.
- CORONA RADIATA.** A fan-shaped band of fibers which radiate from the internal capsule out to the cortex of the cerebral hemispheres.
- CORONARY LIGAMENT.** A ligament which attaches the liver to the diaphragm.
- CORONOID.** A dermal bone of the mandible.
- CORPORA BIGEMINA.** Two small eminences (optic lobes) on the roof of the mesencephalon, serving as visual centers.
- CORPORA QUADRIGEMINA.** Two pairs of small rounded eminences on the roof of the mesencephalon of mammals, corresponding to the corpora bigemina of other vertebrates.
- CORPUS CALLOSUM.** A large band of commissural fibers connecting the two cerebral hemispheres.
- CORPUS CAVERNOSUM.** Erectile tissue of the penis.
- CORPUS LUTEUM.** The scar tissue left on the ovary after the rupture of an egg follicle. It has endocrine functions.
- CORPUS RESTIFORME.** A nerve tract extending from the medulla to the cerebellum. Also called the posterior peduncle.
- CORPUS STRIATUM.** A ventral mass of gray and white matter, in the telencephalon.
- CORTEX.** The outer layer of a structure, such as the brain, kidney, or adrenal.
- CORTIN.** A hormone from the cortex of the adrenal gland.
- COSMINE.** Type of dentine with dentinal tubules in clusters, with channels opening on the surface by pores.
- COTYLOID.** A small triangular bone in the acetabulum of young mammals.
- COWPER'S GLAND.** Glands opening into the urethra of mammals.
- CRIBRIFORM PLATE.** The ethmoid or sieve-bone, with its minute openings for the twigs of the olfactory nerve.
- CRICOID.** A ring-like cartilage of the larynx.
- CRISTAE ACUSTICAE.** Sensory patches in the ampullae of the semicircular canals of the inner ear.
- CRURA CEREBRI.** Nerve bands connecting the cerebellum and posterior parts of the brain with the anterior part.
- CTENOID.** Scales of bony fishes with spiny outer margins.
- CUBOID (TARSALIA 4 + 5).** A bone of the distal tarsal row, at the bases of the fourth and fifth metatarsals.
- CUNEIFORM CARTILAGES.** Small cartilages on the anterior ends of the arytenoids of the larynx.
- CUSP.** A conical development on the surface of a tooth.
- CUVIERIAN DUCTS.** A pair of vessels formed by the union of the anterior and posterior cardinals, which empty their blood into the sinus venosus.
- CYCLOID.** Referring to circular or elliptical scales with a smooth edge.
- CYCLOSPONDYLOUS.** Referring to vertebral centra, in which the calcifications around the notochord are in concentric rings.
- DECIDUA.** The membranous structures formed in the uterus during the development of the fetus. They are discarded at birth.
- DECUSSATION.** The crossing of a band of fibers in the brain connecting unlike parts from one side of the brain to another (optic tract, pyramids).
- DEITER'S CELLS.** Specialized cells of the organ of Corti (ear).
- DELTOID.** An extensor muscle of the upper arm.

- DENDRITES.** Processes of a neuron that conduct impulses towards the cell.
- DENTARY.** The dermal bone which forms the anterior part of the mandible; the entire mandible of mammals.
- DENTINE.** A hard mesodermal material of teeth and some scales.
- DEPRESSOR.** A muscle that lowers a structure.
- DEPRESSOR MANDIBULAE.** A muscle that opens the jaw. Also called the digastric.
- DERMAL PLATES.** Membranous bones of the skin.
- DERMIS.** The deep layer of the skin; the corium.
- DERMOCCIPITAL.** Dermal bone of the skull posterior to the parietals that may fuse with supraoccipital.
- DERMOCRANIUM.** Bony plates covering the head or skull of lower vertebrates, and also part of skull derived from these plates in higher vertebrates.
- DEUTERENKEPHALON.** The posterior portion of the early embryonic brain, including the mesencephalon and rhombencephalon.
- DIAPHRAGM.** A muscular partition which in mammals separates the pericardial and pleural cavities from the abdominal cavity.
- DIAPOPHYSIS.** A process on the neural arch of a vertebra, or a part of the transverse process, forming an articulation for the tubercular head of the rib.
- DIAPSID.** Skull with two temporal openings, one of the synapsid type and the second of the parapsid type.
- DIARTHROSIS.** Free movable joints between bones, with articular surfaces lined with synovial membrane.
- DIATEMA.** A space in the jaw without teeth (rodents).
- DIASTOLE.** The relaxed condition of the heart and arteries.
- DIENCEPHALON.** A region of the forebrain between the telencephalon and mesencephalon.
- DIGASTRIC.** A depressing muscle of the jaw; the depressor mandibulae.
- DIGITIGRADE.** Referring to animals that walk on their toes.
- DIPHYCERCAL.** A primitive, symmetrical fish tail, in which the vertebral column extends straight to the tip.
- DIPHYODONT.** Conditions in which a first set of teeth is replaced by a second set.
- DIPLOSPONDYLOUS.** Referring to vertebrae with double centra.
- DISCUS PROLIGERUS.** A small group of cells that attach the egg to the wall of the Graafian follicle, in the ovary.
- DIVERTICULUM.** A blind pouch or sac, branching off from a main structure; e.g., vermiform appendix.
- DORSAL.** The back or towards the back.
- DUCTUS ARTERIOSUS.** A vestige of the sixth aortic arch, which sometimes persists in tetrapods; ductus Botalli.
- DUCTUS BOTALLI.** See ductus arteriosus.
- DUCTUS PANIZZAE.** Opening between the aortic trunks in some reptiles (Crocodilia).
- DUODENUM.** Proximal end of the small intestine.
- DURA MATER.** The tough, fibrous outer protective covering of the central nervous system.
- ECTEPICONDYLAR FORAMEN.** A small foramen piercing the lateral side of the humerus, at the distal end.
- ECTOCUNEIFORM (TARSALE 3).** A bone of the distal tarsal row at the base of the third metatarsal.

- ECTODERM.** The outer germ layer.
- ECTOPTYRGOID.** One of the pterygoid bones in fishes and reptiles.
- EFFECTOR.** An organ of the nervous system that responds.
- EFFERENT.** Conducting away from a structure, as efferent arteries from gills, efferent nerve fibers from brain to muscles, etc.
- ENAMEL.** A hard, shiny material covering the dentine of teeth and scales.
- ENDOCARDIUM.** The lining of the heart.
- ENDOCRINE GLANDS.** Ductless glands.
- ENDODERM.** The inner germ layer lining the primitive gut.
- ENDOLYMPH.** A fluid that fills the membranous ear.
- ENDOLYMPH DUCT.** A duct leading from the membranous ear to the top of the skull, or ending in lymph spaces of the skull.
- ENDOLYMPH FOSSA.** A depression on the dorsal region of the shark's head, into which the endolymph and perilymph ducts open.
- ENDOSKELETON.** The internal skeleton of vertebrates.
- ENDOSTYLE.** A ciliated groove on the ventral wall of the pharynx in *Amphioxus*.
- ENDPLATE.** The termination of a motor nerve fiber in a muscle.
- ENTEPICONDYLAR FORAMEN.** A small foramen piercing the mesial side of the distal end of the humerus.
- ENTERON.** Cavity of the primitive gut.
- ENTOCUNEIFORM (TARSALE 1).** A bone of the distal row of tarsals, at the base of the first metatarsal.
- ENZYME.** An organic substance which brings about a chemical reaction but is not consumed by it.
- EPAXIAL.** Dorsal to the axis.
- EPAXIAL MUSCLES.** Dorsal division of myomeric muscles.
- EPENDYMA CELLS.** Cells forming the thin membrane which lines the ventricles of the brain.
- EPIBRANCHIAL.** An element of the branchial arch.
- EPICARDIUM.** The covering of the heart.
- EPICORACOID.** A median element of the shoulder girdle.
- EPIDERMAL TEETH.** Tooth-like structures formed from ectoderm; e.g., in cyclostomes, monotremes.
- EPIDERMIS.** The ectodermal, outer layer of the skin.
- EPIDIDYMIS.** The coiled anterior end of the Wolffian duct and the vas efferens, in the male genital system.
- EPIGLOTTIS.** A cartilaginous flap which protects the opening of the glottis.
- EPIHYAL.** An element of the hyoid arch.
- EPIMERE.** The dorsal division of the embryonic mesodermal somite.
- EPINEPHRIN.** The hormone from the medulla of the adrenal gland.
- EPINEURAL BONES.** Small membrane bones, often very numerous, that are formed in the myosepta near the neural arches in fishes.
- EPIOTIC.** The most dorsal of the otic bones forming the capsule of the ear.
- EPIPHYSEAL FORAMEN.** A small opening in the chondrocranium of the shark for the epiphysis or pineal structure.
- EPIPHYSIS.** (a) A term applied to the pineal body. (b) Part of a long bone that ossifies separately and later joins the main structure. (Olecranon process.)
- EPIPLEURAL BONES.** Small membranous bones formed in the horizontal septum in fishes.
- EPIPTYRGOID.** A rod-like skull bone, extending from the pterygoid to the parietal in lacertilians; columella cranii. Probably alisphenoid of mammals.

- EPIPUBIC.** One of a small pair of bones that support the marsupium in the marsupials. They are on the anterior border of the pubics.
- EPISTERNUM.** A median element sometimes present on the ventral side of the sternum; interclavicle.
- EPISTROPHEUS.** The second cervical vertebra; axis.
- EPITHALAMUS.** The dorsal region of the thalamus.
- EPITHELIAL BODIES.** Small epithelial glands, formed in connection with the visceral clefts.
- EPOÖPHORON.** A vestige of the mesonephros, in the female genital system.
- ERYTHROCYTES.** Red blood corpuscles.
- ESOPHAGUS.** The region of the digestive tube between the pharynx and the stomach; gullet.
- ESTRONE.** The ovarian follicular hormone, also termed theelin or estrin, which produces growth in uterus and vagina, cornification of the vaginal epithelium, and the phenomenon of estrus.
- ESTRUS.** Period of sexual cycle in females.
- ETHMOID BONE.** An ossification of the ethmoid plate of the nasal cavity.
- ETHMO-TURBINALS.** Bones of the nasal cavity, associated with the ethmoid.
- EUSTACHIAN TUBE.** A passage between the cavity of the middle ear and the pharynx; auditory tube.
- EUSTACHIAN VALVE OF HEART.** (valvulae venae cavae.) A semilunar fold in the right atrium between the entrance of the post cava and the atrioventricular opening.
- EXOCCIPITAL.** One of a pair of lateral bones forming a part of the occipital region of the skull.
- EXOSKELETON.** The external skeleton derived from skin.
- EXTENSOR DIGITORUM COMMUNIS.** The common extensor of the digits.
- FABELLAE.** Small tendon bones on the posterior side of the knee.
- FACET.** A small articulating surface on a bone.
- FACIAL NERVE.** The seventh cranial nerve.
- FALCIFORM LIGAMENT.** A fold of the peritoneum attaching the liver to the ventral body wall.
- FALCIFORM PROCESS.** A sickle-shaped process in the eyes of fishes.
- FALLOPIAN TUBES.** The anterior region of the oviducts in mammals.
- FALX CEREBRI.** A longitudinal fold of the dura mater which extends between the lobes of the cerebral hemispheres. It is sometimes ossified.
- FASCIA.** Connective tissue covering and binding parts of muscles.
- FASCICULUS.** A bundle of nerve fibers in the brain, that may have different functional connections.
- FASTIGII NUCLEUS.** A nerve nucleus in the cerebellum.
- FEMUR.** The thigh bone of the leg.
- FENESTRA.** Openings, as in the skull. Larger than foramina.
- FENESTRA COCHLEA.** (Fenestra rotundum, tympani, round window.) Membrane-covered foramen between the middle ear and the cochlea.
- FENESTRA OVALE.** (Fenestra vestibuli, oval window.) Foramen through which the stapes transmits its vibrations to the inner ear.
- FERTILIZATION.** The union of the nuclei of the male and female gametes, the result being a zygote.
- FETUS.** Unborn young after reaching the adult form.
- FIBER OF A NERVE.** The slender process of a neuron.

- FIBRILLAE.** Fine threads in cells; e.g., in nerve and muscle cells.
- FIBRIN.** An insoluble, thread-like material produced in coagulating blood.
- FIBRINOGEN.** A soluble protein which forms the fibrin threads and thus causes the coagulation of the blood.
- FIBULA.** The outer shin bone.
- FIBULARE.** A bone of the proximal row of the tarsus, articulating with the fibula; calcaneum.
- FILIPLUMES.** Hair-like feathers.
- FIN-FOLD THEORY.** The theory which derives the fins, both paired and single, from folds of the body wall.
- FIN-RAYS.** The horny supports of fins.
- FISSURE.** A deep fold in the cerebral cortex that involves the whole brain wall.
- FLEXION.** The act of bending.
- FLEXOR DIGITORUM PROFUNDUS.** A deep flexor of the thigh.
- FLEXURE OF BRAIN.** Bends in the neural tube of vertebrate brain.
- FLOCCULUS.** A small lateral lobe of the cerebellum.
- FOLIATE PAPILLAE.** Small projections on the side of the tongue, associated with taste buds.
- FOLLICLE.** A small cavity.
- FOLLICULAR CELLS.** Cells surrounding the ovum while in the Graafian follicle.
- FONTANELLE.** A space between bones of the skull, closed by a membrane.
- FORAMEN.** A small opening; e.g., in bone.
- FORAMEN MAGNUM.** The large foramen surrounded by the occipital bones of the skull, through which the spinal cord joins the brain.
- FORAMEN OF MONRO.** One of the openings between the third and lateral ventricles of the brain.
- FORAMEN PANIZZAE.** An opening between the aortic trunks as they leave the heart; e.g., in *Alligator*.
- FORAMEN TYMPANI.** The round, window-like opening, closed by a membrane between the inner and middle ear; foramen rotundum.
- FORAMEN VESTIBULI.** The stapedial foramen, between the middle and inner ear; foramen ovale.
- FORNIX.** A band of nerve fibers in the cerebral hemispheres associated with smell.
- FOSSA RHOMBOIDALIS.** A cavity on the dorsal side of the myelencephalon.
- FOVEA CENTRALIS.** A spot in the macula lutea of the retina, in which sight is most intense.
- FRONTAL.** One of paired bones in the frontal region of the skull.
- FRONTOPARIETALS.** The joined frontal and parietal bones in the skull of the frog.
- FUNDUS.** The bottom or base of the internal surface of a hollow structure; e.g., of eye, stomach, bladder.
- FUNICULUS.** One of the three divisions of white matter on each side of the spinal cord.
- FURCULA.** The wishbone of birds.
- FUSIFORM.** Spindle-shaped.
- GALL BLADDER.** Storage sac for bile in the liver.
- GANGLION.** A group of nerve cells outside of the central nervous system.
- GANOIN.** The outer shiny layer of a ganoid scale, which is mesodermal in origin.
- GAS GLANDS.** Highly vascularized structures of the swim bladder of fishes, that produce and absorb oxygen.
- GASSERIAN GANGLION.** A ganglion of the fifth cranial nerve; semilunar.

GASTRALIA. Dermal ribs in the abdominal region of some amphibians, reptiles, and birds.

GASTROCOELE. The cavity of the gastrula.

GASTROHEPATIC LIGAMENT. A peritoneal fold attaching the liver to the stomach.

GASTROLITH. Stones in gizzard for grinding food.

GASTRULA. The invaginated, two-layered structure formed from the blastula; a stage in embryonic development.

GEMELLI. Small muscles of the pelvis.

GENICULATES, LATERAL AND MEDIAL. Two small eminences on the roof of the diencephalon.

GENIOGLOSSUS. A muscle of the tongue and mandible.

GENIOHYOID. A muscle of the hyoid and mandible.

GEPHYROCERCAL. A fish tail, internally asymmetrical, but secondarily changed externally to the diphycercal type; e.g., in *Ceratodus*.

GERMINAL DISC. The thin plate or protoplasmic cap on eggs with a large yolk (reptiles or birds), where cleavage first starts.

GILL BARS. Supports of gills.

GILL CLEFTS. Aperture between gills.

GILL-RAKERS. Spines or projections on the branchial arches of fishes.

GIZZARD. A muscular grinding chamber of the stomach, in birds and reptiles.

GLANDS OF LIEBERKÜHN. Tubular glands of the intestine.

GLANS PENIS. The conical enlargement at the distal end of the penis.

GLENOID CAVITY. An articulating cavity in the scapula for the head of the humerus.

GLOMERULUS (OF KIDNEY). A knot of capillaries in the renal corpuscle.

GLOSSOPHARYNGEAL NERVE. The ninth cranial nerve.

GLOTTIS. The opening from the pharynx to the trachea.

GLUTEAL MUSCLES. Extensors of the thigh.

GLYCOGEN. Animal starch, a storage product.

GNATHOSTOMES. Vertebrates possessing jaws, as opposed to the Agnatha (cyclostomes).

GOITER. An enlarged condition of the thyroid gland.

GONAD. The male or female sex gland.

GRAAFIAN FOLLICLE. The vesicular capsule, which surrounds an egg in the ovary.

GRACILIS. A superficial muscle of the thigh.

GRAY MATTER. Part of the central nervous system containing nerve cells.

GROIN. A depressed part of the body between the abdomen and thigh.

GULAR PLATE. A bony plate, sometimes paired, in the throat region of primitive fishes.

GULLET. A region of the digestive tube between the pharynx and stomach.

GYRUS. A ridge. A convolution of the brain.

HABENULA. An olfactory correlation center in the roof of the diencephalon.

HABENULAR COMMISSURE, SUPERIOR. A band of nerve fibers connecting the habenulae.

HAEMAL. Pertaining to blood or blood vessels.

HAEMAL ARCH. A ventral arch on the centra of tail vertebrae of fishes.

HAEMOGLOBIN. The protein-haematin coloring matter of red corpuscles.

HAEMOLYMPH GLANDS. Small glands, containing erythrocytes, associated with the aorta and postcava.

HAGFISH. One of the cyclostomes (*Myxine*).

- HAMATE (CARPALIA 4 + 5).** A bone of the distal carpal row, at the bases of the fourth and fifth metacarpals.
- HAPLODONT.** Referring to teeth consisting of a single cone.
- HARDERIAN GLANDS.** Small glands of the inner angle of the orbit.
- HAVERSIAN CANALS.** Small canals in bone that contain blood vessels, nerve, and lymph vessels.
- HEMIAZYGOS VEIN.** A small vein draining the body wall, a remnant of the supra-cardinals.
- HEMIBRANCH.** The half gill, on one side of the branchial arch.
- HEMIPENES.** The paired organ of copulation in lizards and snakes.
- HENLE'S LOOP.** A loop of the tubule of the renal corpuscle.
- HENSON'S CELLS.** Specialized cells of the organ of Corti, in the ear.
- HEPATIC PORTAL SYSTEM.** A vein conducting the blood from the digestive system to the liver.
- HEPATIC VEINS.** Single or paired veins returning the blood from the liver to the venous system.
- HERBIVOROUS.** Feeding principally on plants.
- HERMAPHRODITE.** An animal with both male and female reproductive organs.
- HETEROCCERAL.** Pertaining to a tail fin, of two unequal lobes, the termination of the axial skeleton being in the larger, upper lobe.
- HETERODONT.** Dentition composed of different kinds of teeth.
- HIPPOCAMPAL COMMISSURE.** A tract of nerve fibers connecting the hippocampi of the two cerebral hemispheres.
- HIPPOCAMPUS.** A fold in the lateral ventricles of the cerebral hemispheres.
- HOLOBRANCH.** A complete gill in which both sides have lamellae or respiratory structures.
- HOMOCERCAL.** Pertaining to a tail fin that is externally symmetrical but internally asymmetrical, since the axial skeleton terminates in the dorsal lobe.
- HOMODONT.** Teeth all of one type.
- HORMONE.** A secretion of the endocrine, or ductless glands.
- HUMERUS.** The bone of the upper arm.
- HYDATID.** A small appendix of the testes, possibly a vestige of the Müllerian duct.
- HYDROSTATIC.** Pertaining to water pressure.
- HYOGLOSSUS.** A muscle of the tongue and hyoid.
- HYOID.** Bone or cartilage derived from ventral part of second visceral arch.
- HYOMANDIBULA.** The dorsal bone of the hyoid arch.
- HYOSTYLIC.** Pertaining to the condition in which the upper jaw is attached to the skull by the hyomandibula.
- HYAPOPHYSIS.** A median ventral process on the vertebral centrum.
- HYPAXIAL.** Ventral to the main axis.
- HYPERSECRETION.** Excessive secretion.
- HYPERTHYROIDISM.** An excessive secretion of the hormones by the thyroid gland.
- HYOBRANCHIAL.** An element of the branchial arch.
- HYOCENTRUM.** Ventral component of the centrum.
- HYOCCONE.** Posterior inner cusp of an upper molar tooth.
- HYOGLOSSAL.** The twelfth cranial nerve.
- HYOPHYAL.** An element of the hyoid arch, between the cerato- and basihyal.
- HYPOMERE.** The ventral region of the mesodermic pouches (embryology).
- HYPOPHYSIS.** A ductless gland on the ventral region of the diencephalon (pituitary body).
- HYPOSECRETION.** Secretion below the normal amount.

- HYPOTHALAMUS.** The ventral region of the diencephalon, the floor of the third ventricle.
- HYPOTHYROIDISM.** A decreased thyroid secretion.
- HYPSELODONT.** Referring to molar teeth with high crowns; e.g., in the cow.
- HYPURAL BONES.** The expanded haemal bones in the tail of teleosts.
- ICHTHYOPTERYGIUM.** Skeleton of the paired fins of fishes.
- ILEUM.** The posterior part of the small intestine.
- ILIAC VEINS.** The vein returning blood from the posterior limb.
- ILIOPSOAS.** A muscle flexing the femur.
- ILIUM.** The dorsal bone of the pelvic girdle, which articulates with the sacral vertebrae.
- INCISIVE CANAL.** A canal posterior to the incisor teeth, present in most mammals.
- INCISORS.** The cutting teeth of the anterior part of the mandible and of the premaxilla of mammals.
- INCUS.** An ossicle of the mammalian middle ear.
- INFUNDIBULUM (BRAIN).** A small funnel-like structure on the ventral side of the diencephalon, closely associated with the hypophysis.
- INFUNDIBULUM (LUNG).** A vesicle of the lung with its alveoli.
- INNER EAR.** The inner chamber of the ear containing the membranous labyrinth.
- INSCRIPTIO TENDINEA.** The remains of myocommata that appear on certain muscles; e.g. on the rectus abdominis, digastric.
- INSERTION.** Attachment of a muscle to a movable part.
- INSULA OF REIL.** A lobe of the cerebrum that is covered by the temporal lobe.
- INSULIN.** A hormone from the islets of Langerhans, in the pancreas.
- INTERARCUALES.** Small muscles of the gill arches.
- INTERCALARIES.** Plates formed between neural arches of elasmobranchs.
- INTERCALARIUM.** The third Weberian ossicle. (*See* Weberian ossicles.)
- INTERCLAVICLE.** A small median element anterior to the sternum; episternum.
- INTERCOSTALS.** Small muscles between ribs.
- INTERDORSALIA.** A part of a sclerotome concerned in the formation of vertebrae.
- INTERHYAL.** An element of the hyoid arch.
- INTERMEDIUM.** The median bone of the proximal carpal and tarsal row.
- INTERNAL CAPSULE.** A band of nerve fibers passing through the corpus striatum of the telencephalon.
- INTERNAL SECRETION.** A secretion of the ductless glands.
- INTEROPERCULAR.** One of the gill-covering bones of fishes.
- INTERPARIETAL.** A small dermal bone on the mid-dorsal face of the skull that usually joins with the supraoccipital but may remain separate.
- INTERRENAL BODY.** Bodies, separate in fishes, which join in tetrapods, forming the cortex of the adrenal gland.
- INTERSTITIAL CELLS.** Specialized cells of the testes that produce hormones.
- INTERTEMPORAL.** A bone in the skull of amphibians and reptiles.
- INTERVENTRALIA.** Part of a sclerotome concerned in vertebra formation.
- INTERVENTRICULAR FORAMEN.** Paired foramina connecting the third with the lateral ventricles of the brain; foramina of Monro.
- INVAGINATION.** The drawing inwards of a portion of a hollow structure. (*Invagination of lens.*)
- INVERTASE.** A ferment acting upon sugars.
- IRIS.** A contractile, pigmented disc which is a part of the choroid coat, placed between the cornea and the lens of the eye.

- ISCHIUM.** The posterior, ventral bone of the pelvic girdle.
- ISLETS OF LANGERHANS.** Spherical, or oval cells scattered throughout the pancreas.
- ISODONT.** Dentition in which teeth are all alike.
- ITER.** Canal connecting the third and fourth ventricles of the brain of higher vertebrates.
- JACOBSON'S ORGAN.** An accessory olfactory organ, associated with the nasal cavities, may be associated with taste.
- JEJUNUM.** A part of the small intestines between the duodenum and the ileum.
- JUGAL.** A skull bone of the zygomatic arch; malar, zygomatic.
- KATABOLISM.** The destructive forces of metabolism.
- KIDNEY.** The organ of excretion in amniotes. The term is also used for the organs of excretion of lower types.
- LABIAL CARTILAGES.** Extra cartilages along the jaws of sharks.
- LABYRINTH, BONY.** Bony covering of the membranous ear.
- LABYRINTH, MEMBRANOUS.** Membranous part of the inner ear.
- LACRIMAL.** A bone of the anterior region of the orbit, usually pierced by the lacrimal duct.
- LACUNAE.** Small cavities; e.g., those of bone.
- LAGENA.** An outgrowth from the sacculus of the inner ear.
- LAMELLA.** A plate-like structure; e.g., respiratory plates of gills.
- LAMINA TERMINALIS.** The anterior wall of the third ventricle of the brain.
- LANUGO.** The coat of hair present on embryos. Usually shed before birth.
- LARNYX.** Voice box. Structure enclosing the vocal cords and the entrance to the lungs.
- LATERAL LINE.** A line of sensory structures along the side of fishes.
- LATISSIMUS DORSI.** A muscle extending from the vertebral column to the humerus.
- LEUCOCYTES.** White blood corpuscles.
- LEVATOR.** A muscle that raises the part to which it is attached.
- LINEA ALBA.** A connective tissue, white line, to which the abdominal muscles are attached. (Midline of body.)
- LINGUAL.** Pertaining to the tongue.
- LIPASE.** A digestive ferment that acts on fats.
- LOBULE.** A small lobe, as in the liver, lung, kidney.
- LONGISSIMUS DORSI.** A group of epaxial muscles extending along the back.
- LOPHODONT.** Pertaining to molars with cross ridges and crests on the grinding surface.
- LORENZINI'S AMPULLAE.** Mucus-filled sense organs on the snout of elasmobranchs.
- LUMEN.** A cavity in a hollow structure.
- LYMPH.** A colorless, coagulating fluid of the lymph vessels.
- LYMPH HEARTS.** Pulsating sacs in the lymphatic systems of lower vertebrates.
- LYMPHOCYTES.** White blood corpuscles of the lymph system.
- MACULAE ACUSTICAE.** Sensory patches of the utricle and saccule of the inner ear.
- MACULA LUTEA.** A spot on the retina where vision is most distinct.
- MALAR BONE.** Cheek bone, zygomatic.
- MALLEUS.** The outer ossicle of the mammalian middle ear.
- MALPIGHIAN CORPUSCLE.** The unit of structure of the organ of excretion (the renal corpuscle).

- MALPIGHIAN LAYER.** The growing layer of the epidermis, which is in contact with the corium.
- MAMMARY GLANDS.** The milk glands of mammals.
- MAMMILLARY BODY.** One of a small, paired spherical mass on the ventral side of the brain, just posterior to the tuber cinereum.
- MANDIBULAR ARCH.** The visceral arch from which the jaws are formed.
- MANDIBULAR CARTILAGE.** Meckel's cartilage, the lower jaw of sharks, and the cartilage on which the membrane bones are applied in other vertebrates.
- MANUBRIUM.** The anterior part of the sternum.
- MASSA INTERMEDIA.** A band of fibers connecting the walls of the third ventricle of the brain; soft commissure, commissura mollis.
- MASSETER.** An adductor muscle of the mandible.
- MATURATION PROCESS.** The completion of the ripening of the sex cells by a reduction of the number of chromosomes.
- MAXILLA.** A bone of the upper jaw, posterior to the premaxilla.
- MAXILLARY NERVE.** A branch of the fifth cranial nerve.
- MAXILLO-TURBINALS.** Turbinal bones in the nasal cavity attached to the maxilla.
- MECKEL'S CARTILAGE.** The lower half of the mandibular arch, the lower jaw of cartilaginous fishes.
- MEDIASTINUM.** A median septum between the lungs, formed by the pleural membranes.
- MEDULLA.** The central part of an organ or tissue; e.g., kidney, adrenal gland.
- MEDULLA OBLONGATA.** The posterior region of the brain or myelencephalon.
- MEDULLATED.** Covered with a marrow-like substance (medullated nerves).
- MEIBOMIAN GLANDS.** Oil glands of the eyelids.
- MELANISTIC.** Excessively pigmented.
- MEMBRANA BASILARIS.** The floor of the scala media of the inner ear.
- MEMBRANOUS BONE.** Bones developed from skin.
- MEMBRANOUS EAR.** The entire membranous structure of the inner ear.
- MENINGES.** The membranes which envelop the brain and spinal cord.
- MENTOMECKELIAN CARTILAGE.** The anterior tip of the Meckelian cartilage, ossified in the Anura.
- MESAXONIC.** Referring to a type of foot in which the main axis passes through the third digit.
- MESENCEPHALON.** The midbrain.
- MESENCHYME.** Mesodermal cells migrating from the splanchnic walls of the mesomere and from the somatic walls of myotomes.
- MESENTERIES.** Folds of the peritoneal lining which support organs of the visceral cavity.
- MESETHMOID.** A median element of the nasal region, forming the cribriform plate.
- MESOCOEL (BRAIN).** An extension of the primitive ventricle of the mesencephalon into the optic lobes.
- MESOCORACOID.** An element of the shoulder girdle.
- MESOCUNEIFORM.** A bone of the distal row of the tarsus, at the base of the second metatarsal; tarsale 2.
- MESODERM.** The middle germ layer.
- MESOMERE.** The median region of the mesodermal pouch.
- MESONEPHROS.** The functional organ of excretion in fishes and amphibians, and an embryological structure of amniotes.
- MESOPTERYGIUM.** The median, basal cartilage of the pectoral fin in elasmobranch.
- MESORCHIIUM.** The mesentery supporting the testes.

MESORECTUM. Mesentery of the rectum.

MESOVARIUM. The mesentery of the ovaries.

MESOTHELIUM. A part of the mesoderm that lines the coelom and gives rise to muscle and connective tissue.

METABOLISM. The constructive and destructive chemical changes occurring in living organisms.

METACARPUS. Bones of the hand between the phalanges and the carpus or wrist.

METACOEL. (1) The body cavity formed by the hollow hypomeres. (2) An extension of the fourth ventricle into the cerebellum.

METACONE. The postero-external cusp of upper molar teeth (mammals).

METACONID. The postero-internal cusp of lower molar teeth (mammals).

METAMERE. A body segment.

METAMERISM. The linear repetition of parts.

METAMORPHOSIS. Striking changes between the immature and adult form as tadpole to frog, caterpillar to butterfly.

METANEPHROS. The kidney of amniotes.

METAPTERYGIUM. The posterior, basal cartilage of the shark fin.

METATARSUS. Bones of the foot, between the phalanges and the ankle.

METENCEPHALON. The anterior part of the rhombencephalon of the brain, includes cerebellum.

MIDDLE EAR. The middle chamber of the tetrapod ear, containing the ossicles.

MITRAL VALVE. A valve between the left atrium and left ventricle.

MOLAR TEETH. The posterior grinding teeth.

MONIMOSTYLIC. Referring to a condition of the skull in which the quadrate is fixed and immovable.

MONOPHYODONT. Condition where there is but one set of teeth in a lifetime.

MONOSPONDYLY. Type of vertebra with single centrum formed of elements from two somites.

MUCOSA. The inner lining of the intestine; a mucous membrane.

MÜLLERIAN DUCTS. The oviducts of the female reproductive system.

MULTICUSPIDATE. Molars with many cusps.

MULTITUBERCULAR. Referring to molar teeth in which the crown has many tubercles.

MYELENCEPHALON. The posterior division of the brain, which joins the spinal cord; the medulla oblongata.

MYELIN SHEATH. A covering around the axis-cylinder process of some nerves.

MYLOHYOID. A superficial muscle between the mandibles.

MYOCOMMATA. Sheets of connective tissue between muscle segments.

MYOMERE. A muscle segment.

MYOSEPTUM. A sheet of connective tissue between myotomes or muscle segments.

MYOTOME. A muscular segment of primitive vertebrates and embryos.

MYXEDEMA. A condition in which the skin becomes swollen, probably because of abnormal conditions of the thyroid gland.

NARES. Nostrils.

NARES, INTERNAL. The openings connecting the nasal cavity with the pharynx.

NASAL CONCHAE. The bony scrolls on the walls of the nasal cavity.

NASAL SAC. The cavity of the olfactory organ in fishes.

NASO-TURBINAL. Cartilage or bone in the nasal cavity, arising from the nasal bones.

NEPHRIDIUM. The excreting tubules and ducts of the organ of excretion.

- NEPHROGENIC CORD.** A mass of cells along the dorsal body wall destined to form the kidney tubules.
- NEPHROSTOME.** The openings of the nephridial tubules into the body cavity.
- NERVE.** A bundle of conducting fibers, outside of the central nervous system.
- NERVE FIBER.** A thread-like process of a neuron.
- NERVE NUCLEUS.** A specialized nerve center in the central system.
- NERVE TRACT.** A number of nerve fibers of like origin, termination, and function.
- NEURILEMMA.** The outer sheath of a peripheral nerve fiber.
- NEURITE.** The process of a nerve cell that carries the impulse away from the neuron; axon.
- NEUROCRANIUM.** The cartilaginous or bony case surrounding the brain and sense organs.
- NEUROGLIA.** Supporting cells in nerve tissue.
- NEUROMASTS.** Groups of sensory cells in the lateral line of fishes.
- NEURON.** A nerve cell and processes. The unit of structure of the nervous system.
- NEUROPORE.** The anterior opening of the brain cavity in an embryo.
- NICITATING MEMBRANE.** A third eyelid, a thin membrane that may appear in all vertebrates except the mammals, where it is a vestige in the inner angle of the eye.
- NOTARIUM.** Joined thoracic vertebrae in reptiles and birds.
- NOTOCHORD.** A supporting axial rod appearing in some stage of all chordates.
- OBLIQUE CAPITIS.** A muscle between the vertebral column and the skull.
- OBTURATOR FORAMEN.** A foramen in the pelvic girdle.
- OBTURATOR INTERNUS and EXTERNUS.** Muscles between the pelvis and femur.
- OCCIPITAL BONES.** The skull bones forming the posterior part of the skull and surrounding the foramen magnum.
- OCCIPITAL VERTEBRAE.** Vertebrae that fuse with the cranium and form the posterior region.
- OCULOMOTOR.** The third cranial nerve.
- ODONTOID PROCESS.** An anterior, tooth-like process on the centrum of the axis, also called the dens.
- OLECRANON PROCESS.** A curved process on the proximal end of the ulna.
- OLFACTORY BULB.** The anterior prolongation of the telencephalon of the brain, containing the olfactory center. It is small and ventral in mammals.
- OLFACTORY NERVE.** The first cranial nerve.
- OLIVE.** A nerve nucleus of the myelencephalon. The olivary nucleus.
- OMASUM (PSALTERIUM).** Third division of the stomach of ruminants.
- OMENTUM.** Fold of the peritoneum covering the abdominal organs.
- OMOXYOID.** A muscle of the hyoid and scapula.
- OMPHALO-PLACENTA.** A pseudo-placenta formed from the yolk sac.
- OÖCYTE.** An ovum before maturation.
- OPERCULAR BONES.** The gill-covering bones of fishes.
- OPERCULUM OF FISHES.** Bony cover over the gills.
- OPHTHALMICUS PROFUNDUS.** The deep branches of cranial nerves five and seven.
- OPHTHALMICUS SUPERFICIALIS.** The superficial branches of cranial nerves five and seven.
- OPISTHOCOELOUS.** Referring to a type of vertebra in which the posterior end of the centrum is concave.
- OPISTHONEPHROS.** Adult mesonephric kidney which extends full length of body cavity.

- OPISTHOTIC.** The posterior bone of the ear capsule.
- OPTIC CUP.** The double-walled structure formed as an outpouching from the brain, and occurring in the formation of the eye.
- OPTIC NERVE.** The second cranial nerve.
- OPTIC VESICLES.** The hollow outpouching from the forebrain, that forms parts of the eye.
- ORA SERRATA.** The anterior edge of the retina where it ceases to be sensory, but is continued as a thin membrane. This difference in structure forms a wavy line around the inside of the eye.
- ORBITOSPHEOID.** A bone of the brain case containing the optic foramen.
- ORGAN OF CORTI.** The specialized organ of hearing in the scala media of the cochlea.
- ORO-NASAL GROOVE.** The groove between the mouth and nose in elasmobranchs.
- OS CORDIS.** An irregular bone at the base of the aorta of ungulates.
- OSMOTIC PRESSURE.** The phenomenon that gives rise to transfusion and osmosis, when two liquids such as salt and fresh water are separated by a permeable partition such as an animal membrane.
- OS PRIAPI.** The penis bone, present in some mammals.
- OSTIUM TUBAE.** The anterior opening of the oviduct to the body cavity.
- OTOCONIA.** Otoliths, or ear dust, calcium carbonate crystals covering the sensory patches of the inner ear.
- OTOLITHS.** Calcareous particles, or "ear stones," in the endolymph of the membranous labyrinth of the ear.
- oviduct.** Duct along which the egg travels to get from the ovary to the outside.
- OVIPAROUS.** Referring to animals that lay eggs.
- OVOVIVIPAROUS.** Referring to a condition in which the eggs are retained in the oviducts until hatched.
- OVULATION.** The forming of the egg and its discharge from the Graafian follicle.
- PALATE, HARD.** A secondary mouth roof, formed by the mesial extension of the palatines and maxillae.
- PALATINE.** A bone of the basicranial region of the skull.
- PALATINE GLANDS.** Glands of the palate region.
- PALATINE TONSILS.** Lymphoid structures, just posterior to the openings of the auditory tubes.
- PALATOQUADRATE (PTERYGOQUADRATE).** The dorsal half of the mandibular arch.
- PALLIAL COMMISSURE.** A connecting nerve tract of the pallial region of the cerebral hemispheres.
- PALLIUM.** The roof of the telencephalon.
- PAPILLA.** A small projection.
- PAPILLA LAGENAE.** The auditory area of the lagena in reptiles and birds.
- PARACHORDALS.** A pair of cartilaginous plates, paralleling the notochord in skull development.
- PARACONE.** The antero-external cusp of an upper molar tooth.
- PARACONID.** The antero-internal cusp of a lower molar tooth.
- PARADIDYMS.** Remnants of mesonephric tubules associated with the genital organs of male mammals.
- PARAFLOCCULUS.** A secondary lateral lobe of the metencephalon, on the side of the cerebellum.
- PARAPHYSIS.** A choroid plexus outgrowth from the anterior region of the dien-cephalon roof.

- PARAPOPHYSIS.** The lateral process of a vertebra, articulating with the capitular head of a rib. It also forms part of a transverse process.
- PARAPSID.** Skull having a single temporal opening, the upper edge being formed by the parietal.
- PARASPHENOID.** A median bone of the basicranial region, prominent in fishes and amphibians.
- PARASYMPATHETIC SYSTEM.** The cranial and sacral nerve supply of the autonomic system.
- PARATHYROID GLAND.** An endocrine gland associated with the thyroid.
- PARAXONIC.** Referring to feet in which the main axis passes between the third and fourth digits; e.g., those of cow, deer, pig.
- PARIETAL EYE.** An anterior eye-like structure on the roof of the diencephalon, prominent in some reptiles.
- PAROÖPHORON.** Rudimentary tubules of the mesonephros, associated with the genital organs of female mammals.
- PAROTID GLAND.** A large salivary gland usually anterior to the ear.
- PATELLA.** A sesamoid bone of the knee (kneecap).
- PAVEMENT TEETH.** Peculiar flat teeth of some fishes.
- PECTEN.** A comb-like structure extending from the retina to the lens in the eyes of reptiles and birds.
- PECTINEUS.** A small, slender adductor muscle of the thigh.
- PECTORAL.** A term referring to shoulder girdle and associated structures.
- PECTORALIS, MAJOR AND MINOR.** An adductor muscle of the thigh.
- PEDUNCLE, ANTERIOR.** A tract of fibers connecting the cerebellum with the mesencephalon; brachium conjunctivum.
- PEDUNCLE, MIDDLE.** A tract of nerve fibers forming a band across the ventral surface of the metencephalon, and connecting the cerebellar lobes; brachium pontis.
- PEDUNCLE, POSTERIOR.** A tract of nerve fibers connecting the myelencephalon with the cerebellum; corpus restiforme.
- PELVIS.** A term referring to the posterior girdle and associated structures.
- PENIS.** The male organ of copulation in higher vertebrates.
- PENIS BONE.** A bone present in the penis of some mammals; os priapi.
- PEPSIN.** A digestive ferment of the stomach.
- PERICARDIAL CAVITY.** The enclosed cavity in which the heart lies.
- PERICARDIAL SAC.** The membranous wall of the pericardial chamber.
- PERICARDIUM.** A membrane enclosing the heart.
- PERILYMPH.** The fluid surrounding the membranous labyrinth of the ear.
- PERISTALSIS.** A wave-like motion of the intestine or any structure, caused by the alternate contraction of the circular and longitudinal muscles, which thus forces the contents along the tube.
- PERITONEUM.** The lining of the peritoneal or body cavity.
- PEYER'S PATCHES.** Lymph nodes forming aggregates in the lining of the intestine.
- PHALANX.** A bone of the digits of vertebrates.
- PHARYNGEAL TONSILS.** Nodes of lymph tissue, just posterior to the internal nares.
- PHARYNGOBRANCHIAL.** An element of the branchial arch.
- PHARYNX.** A short region of the digestive tube between the mouth and the esophagus.
- PHOTOPHORE.** A luminous or light-emitting organ of fishes.

- PHYSOSCLISTOUS.** Referring to fishes in which the pneumatic duct between the swim bladder and the digestive tube is closed.
- PHYSOSTOMOUS.** Referring to fishes in which the pneumatic duct between the swim bladder and the digestive tube remains open.
- PIA MATER.** The innermost covering of the brain and spinal cord.
- PIGEON'S MILK.** A product secreted in the crop of pigeons and fed to the young.
- PINEAL BODY.** The posterior evagination on the roof of the diencephalon, glandular in birds and mammals.
- PINNA.** The projecting part of the outer ear.
- PIRIFORMIS.** A deep muscle of the thigh.
- PISIFORM.** A carpal bone of the proximal series of sesamoid origin.
- PITUITARY GLAND.** An endocrine gland on the ventral side of the diencephalon.
- PITUITRIN.** A hormone from the pituitary gland.
- PLACENTA.** A mammalian structure formed by fetal and maternal tissues, which serves as a medium of exchange for nutritional and excretory products, between the mother and the young.
- PLACODE.** A plate-like region of the ectoderm, from which arise sensory and nervous structures.
- PLACOID SCALE.** A spine-like scale, of elasmobranchs.
- PLANKTON.** Small floating life in water.
- PLANTIGRADE.** Applied to animals that walk on the sole of the foot.
- PLASMA.** The fluid medium of the blood or tissues.
- PLASTRON.** A shield of bone, protecting the ventral side of the body; e.g., turtle.
- PLATYBASIC.** Referring to a type of skull in which the trabeculae do not join in the region between the eyes; e.g., amphibians.
- PECTRUM.** A slender rod, extending from the stapes.
- PLEURA.** The serous lining of the chest cavity, which also invests the lungs.
- PLEUROCENTRUM.** Dorsolateral components (arcualia) of the centrum.
- PLEURODONT.** Referring to teeth ankylosed to the inner side of the jaw.
- PLEURO-PERITONEAL.** The combined pleural and peritoneal cavities.
- PLEXUS.** A network of interlacing blood vessels or nerves.
- PLICA CIRCULARES.** Folds of the inner lining of the intestines.
- PLUMULAE.** Down feathers.
- PNEUMOGASTRIC.** The tenth cranial nerve; vagus.
- POLYPHYODONT.** Having many replacements of teeth.
- PONS.** A band of nerve fibers extending around the ventral side of the metencephalon and connecting the cerebellar hemispheres.
- PORTAL SYSTEM.** Part of the venous system that leads blood to the liver or kidney. Starts in capillaries and ends in capillaries.
- POSTAXIAL.** On the posterior side of the axis.
- POSTCARDINAL.** Large pair of veins carrying blood from the posterior part of body to heart in lower vertebrates.
- POSTCAVA.** A large vein which conducts venous blood from the posterior region of the body to the heart.
- POSTERIOR.** Toward the tail or rear end.
- POSTERIOR CHAMBER (EYE).** A small space between the iris and the lens.
- POSTFRONTAL.** A bone of the skull roof, posterior and lateral to the frontal.
- POSTGANGLIONIC.** Nerve fibers distal to a ganglion.
- POSTORAL.** Posterior to the mouth.
- POSTORBITAL BAR.** A lateral cartilage that extends outward from the chondrocranium, posterior to the orbit.

- POSTTREMATIC.** Posterior side of the gill slit.
- POSTZYGAPOPHYSIS.** An articular process on the posterior region of the neural arch of a vertebra.
- PREARTICULAR.** A bone of the mandible; goniale.
- PREFRONTAL.** A bone of the skull roof, anterior and lateral to the frontal.
- PREGANGLIONIC.** Nerve fibers proximal to a ganglion.
- PREMAXILLA.** A paired bone anterior to the maxillae.
- PREMOLAR.** Teeth between the canines and molars.
- PREOPERCULAR.** The anterior gill-covering bone of fishes.
- PREORAL.** Anterior to the mouth.
- PRESTERNUM.** An element anterior to the sternum.
- PRETREMATIC.** Anterior side of the gill slits.
- PREVOMER.** A bone of the anterior, median region of the skull.
- PREZYGAPOPHYSIS.** An articular process on the anterior region of the neural arch of a vertebra.
- PRIMORDIAL.** Of earliest origin.
- PROCOELOUS.** Referring to a type of vertebra in which the anterior end of the centrum is concave.
- PROCORACOID (PRECORACOID).** The anterior bone of the shoulder girdle.
- PROCTODAEUM.** The ectoderm-lined, posterior end of the digestive tube.
- PROGESTIN (CORPORIN).** A hormone of the follicular cells surrounding the ovum.
- PROLAN.** A gonad-stimulating hormone extracted from the urine of pregnancy.
May be separated into two factors; prolan A, the follicular stimulating factor; and prolan B, the luteinizing factor.
- PRONATION.** Twisting a limb towards the median axis.
- PRONEPHROS.** The primitive head kidney of embryonic life.
- PROÖTIC.** The most anterior of the bones forming the ear capsule.
- PROPTERYGIUM.** The anterior element of the fin base.
- PROSENCEPHALON.** The first primitive brain vesicle.
- PROSTATE GLAND.** A muscular gland of males, surrounding the urethra at its exit from the urinary bladder.
- PROSTATE VESICLE.** A small sac imbedded in the prostate gland, sometimes called the male uterus.
- PROTOCONE.** The inner cusp of an upper molar tooth.
- PROTOCONID.** The external cusp of a lower molar tooth.
- PROTODONT.** Referring to teeth with a primitive, single cone.
- PROVENTRICULUS.** The glandular stomach, anterior to the gizzard in birds and other animals.
- PSALTERIUM.** The third division of the ruminant stomach.
- PTEROTIC.** A cranial bone of fishes that overlies the otic capsule.
- PTERYGOID.** A bone of the basicranial region of the skull.
- PTERYGOID EXTERNUS and INTERNUS.** Small muscles between the pterygoid bone and the mandibles.
- PTERYGOPHORE.** Endoskeletal support of fin.
- PTERYGOPODIA.** A specialized development of the pelvic fin in male sharks.
- PTERYGOQUADRATE (PALATOQUADRATE).** Dorsal half of mandibular arch.
- PTERYLAE.** Feathered tracts in birds.
- PTYALIN.** A digestive ferment of saliva.
- PUBIS.** The anterior, ventral element of the pelvic girdle.
- PULMONARY ARTERY.** A vessel conducting the blood from the heart to the lungs.
- PULMONARY VEIN.** A vessel conducting the blood from the lungs to the heart.

- PULVINAR NUCLEUS.** A visual center of the diencephalon.
- PUPIL.** The opening in the iris of the eye.
- PYGOSTYLE.** Posterior bone of bird vertebral column, made up of fused, caudal vertebrae.
- PYLORIC VALVE.** A muscular valve between the pyloric end of the stomach and the duodenum.
- PYRAMIDS.** A pair of large motor nerve tracts on the ventral side of the brain.
- QUADRATE.** A bone through which the jaw articulates with the skull in all vertebrates except mammals and a few low forms.
- QUADRATOJUGAL.** A bone of the skull, between the jugal and the quadrate.
- QUADRATUS FEMORIS.** A muscle between the ischium and the femur.
- QUADRICEPS EXTENSOR.** A muscle between the pelvis and the femur.
- QUADRITUBERCULAR.** Referring to a molar with four tubercles on the crown.
- QUINTITUBERCULAR.** Referring to a molar with five tubercles on the crown.
- RADIALE.** A bone of the proximal carpal series, articulating with the radius; scaphoid, navicular.
- RADIALS.** Endodermal supporting rays in fish fins.
- RADIUS.** A bone on the thumb side of the forearm.
- RAMUS COMMUNICANS.** Nerve connecting a sympathetic ganglion with a spinal nerve.
- RATHKE'S POCKET.** A small diverticulum from the roof of the mouth, which forms the anterior part of the hypophysis.
- RATITE.** Walking birds having a flat, unkeeled sternum, such as ostrich, emu.
- RECEPTOR.** A receiving sense cell of the nervous system.
- RECTUM.** The posterior terminal region of the alimentary canal.
- RECTUS ABDOMINIS.** Median muscle of ventral abdominal wall.
- RECTUS CAPITIS.** A muscle between the skull and the vertebral column.
- RED BODY.** Gas glands of a simple type present in fishes with open duct to the swim bladder. The gland consists of a secreting epithelium and a capillary network.
- RED GLAND.** The highly developed gas-forming gland, in which the epithelium is thrown into folds and crypts. Present in fishes with a closed airduct.
- RED NUCLEUS.** A center of coordination in the mesencephalon.
- REFLEX ARC.** A chain of neurons which function in a reflex act.
- REISSNER'S MEMBRANE.** A membrane forming the ventral wall of the scala vestibuli of the inner ear.
- REMIGES.** Flight feathers.
- RENAL CORPUSCLE.** The unit of structure of the kidney, or organ of excretion; Malpighian corpuscle.
- RENAL PORTAL SYSTEM.** Veins conducting the blood to the tubules of the kidney.
- RETE MIRABILE.** Regions where arteries or veins break up abruptly into a fine network of capillaries; e.g., swim bladder, glomeruli of kidney.
- RETICULUM.** The honeycomb, or second division of the ruminant stomach.
- RETINA.** The inner sensory coat of the eye.
- RETROLINGUAL GLANDS.** Salivary glands posterior to the tongue.
- RHOMBENCEPHALON.** The third primitive brain vesicle.
- RHOMBOIDEUS.** A muscle between the vertebral column and the scapula.
- RODS AND CONES.** Sensory light receptors of the retina.
- ROSTRUM.** The anterior projection of the chondrocranium of the shark.

ROUND LIGAMENT. A ligament that attaches the ovary to the posterior region of the body cavity; also a ventral ligament of the liver.

RUDIMENTARY. Undeveloped remains of structures.

RUMEN. The paunch, or first stomach of a ruminant.

SACculus. A region of the membranous inner ear.

SACRUM. One or more sacral vertebrae, which form an attachment for the pelvic girdle.

SAGITTAL. A section through a dorsoventral, longitudinal median plane or parallel to it.

SANTORINI'S DUCT. An accessory pancreatic duct.

SARCOLEMMMA. The sheath of a muscle fiber.

SARCOPLASM. The reticular content of a muscle cell.

SARTORIUS. A muscle of the thigh.

SAVI'S VESICLE. Sensory vesicles of some elasmobranchs, somewhat similar to the ampullae of Lorenzini. Associated with the lateral line.

SCALA MEDIA. The median or cochlear duct of the inner ear.

SCALA TYMPANI. The ventral perilymph space of the bony cochlea.

SCALA VESTIBULI. The dorsal perilymph space of the bony cochlea.

SCAPHIUM. The second Weberian ossicle.

SCAPULA. The dorsal bone of the shoulder girdle.

SCLEROTIC BONES. Bones formed in the sclerotic coat of the eye.

SCLEROTIC COAT. The tough, outer, fibrous coat of the eye.

SCLEROTOME. Portion of the mesenchyme or mesodermic cells that form the axial skeleton.

SCROTAL SAC. An external, extra-abdominal sac, containing the testes.

SEBACEOUS GLAND. An oil gland of the skin.

SECODONT. Pertaining to teeth with cutting edges.

SECRETIN. A hormone from the intestinal wall which causes the pancreas to discharge its secretions.

SEGMENTAL STRUCTURES. Structures that are repeated in a linear series; e.g., vertebrae, nerves, blood vessels.

SELENODONT. Referring to molars with a folded surface on the crown, which, with wear, show a crescentic pattern.

SEMICIRCULAR DUCTS. Three ducts of the inner ear concerned in equilibrium.

SEMILUNAR GANGLION. A ganglion of the fifth cranial nerve; Gasserian.

SEMILUNAR VALVES. Small flaps in blood and lymph vessels that prevent a back-flow.

SEMINAL VESICLE. A small storage sac in males, for the storage of sperm; a glandular structure in males of some mammals.

SEMIspINALIS CAPITIS. A muscle between the skull and vertebral column.

SEPTOMAXILLARY. A small bone sometimes developed in the nasal capsule; e.g., in Amphibia.

SEPTUM. A partition.

SEPTUM PELLUCIDUM. A double membrane separating the anterior horns of the lateral ventricles (forebrain).

SEPTUM TRANSVERSUM. A thin partition separating the pericardial from the visceral cavity.

SEROSA. A thin, lining membrane.

SEROUS. Thin, watery.

SERRATUS MAGNUS. A muscle between the vertebral column and ribs.

SERUM. The thin, watery fluid of blood, or lymph, that separates out on coagulation.

SESAMOID. A bone formed in tendons, usually small and rounded in shape.

SHOULDER GIRDLE. The bones of the pectoral girdle.

SINUS VENOSUS. A thin-walled sac, to which the venous blood of lower vertebrates is delivered, before entering the atrium.

SINUSOID. An anastomosing endothelium-lined blood space (liver, spleen, and other organs).

SOMATIC MOTOR FIBERS. Motor fibers to the skin and muscles.

SOMATIC SENSORY FIBERS. Sensory fibers to the skin and external sense organs.

SPHONOTOPLEURE. Fold of mesoderm lining the body cavity.

SPHENETHMOID. One of a pair of bones forming a ring around the olfactory nerve of some amphibians.

SPHINCTER. A circular muscle surrounding an orifice, e.g., mouth, eye, anus.

SPINAL ACCESSORY. The eleventh cranial nerve.

SPIRAL VALVE. A part of the intestine in sharks and lower fishes, in which a fold of the inner lining forms a spiral, thus increasing the area and slowing down the food in its passage through it.

SPLANCHNOCRANIUM. Parts of the skull derived from visceral arches.

SPLENIAL. A small bone of the inner side of the mandible.

SPLENIUS CAPITIS. A muscle between the skull and vertebral column.

SQUAMOSAL. A bone of the posterior side wall of the skull.

STAPEDIUS. A small muscle of the middle ear, attached to the stapes.

STAPES. An ossicle of the middle ear, in contact with the foramen vestibuli.

STERNALIA. Segments of the breastbone or sternum.

STERNEBRA. Segment of the sternum.

STERNOHYOID. A muscle between the hyoid and sternum.

STERNOMASTOID. A muscle between the sternum and the mastoid region of the skull.

STERNUM. The breastbone.

STOMATA OF LYMPH SYSTEM. Small pores or openings between epithelial cells of lymph spaces.

STRATUM CORNEUM. Outer layer of dead cells of epidermis.

STREPTOSTYLIC. Referring to a condition of the skull in which the quadrate is movable.

STYLOGLOSSUS. A muscle between the tongue and the styloid process of the skull.

SUBCARDINALS. Embryonic veins between kidneys that become posterior part of postcardinals.

SUBCLAVIAN. Referring to a vein, artery, or nerve which supplies the anterior fin or fore limb.

SUBLINGUA. Fleishy folds beneath the tongue of some mammals.

SUBLINGUAL GLANDS. Salivary glands below the tongue.

SUBMAXILLARY GLANDS. A pair of salivary glands in the lower jaw region.

SUBMUCOSA. A layer of tissue beneath the mucosa or inner lining of the intestine.

SUBOPERCULAR. One of the ventral gill-covering bones of fishes.

SUBORBITAL RING. A ring of dermal bones around the eye.

SUPERITONEAL. Beneath the peritoneum, or outside the body cavity.

SUBSCAPULARIS. An adductor muscle of the humerus.

SUCCUS ENTERICUS. The digestive juice of the small intestine.

SUDORIPAROUS GLANDS. The sweat glands of the skin.

SULCUS. A groove.

SUPERIOR VENA CAVA. A vein draining the blood from the head region to the heart.

SUPINATION. Twisting a limb outward from the median axis.

SUPRACARDINAL. Vein in reptiles formed from the segmental veins of the post-cardinals.

SUPRACLEITHRUM. A dermal bone dorsal to the cleithrum, in fishes.

SUPRAOCCIPITAL. A median, dorsal bone of the posterior region of the skull.

SUPRAORBITAL. A dermal bone over the orbit of the eye.

SUPRATEMPORAL. A bone of early reptiles, lateral to the parietal.

SUSPENSORY LIGAMENT. A ligament supporting the lens of the eye, etc.

SYMPATHETIC SYSTEM. A division of the involuntary, autonomic nervous system.

SYMPHYSIS. The line of juncture between two bones.

SYMPLECTIC. A bone of the fish skull, lying between the quadrate and the hyomandibula.

SYNAPSE. The place of transmission of impulses between processes of neurons.

SYNAPSID. Skull having a single temporal opening, the upper edge of which is formed by the squamosal and postorbital bones.

SYNARTHROSIS. Immovable joint between bones that tend to fuse.

SYNOVIAL MEMBRANE. The inner layer of tissue, lining the capsules around joints and supplying a lubricating fluid.

SYNSACRUM. A number of fused vertebrae, supporting the pelvic girdle in birds, consisting of lumbar, sacral, and caudal.

SYRINX. A sound-producing structure of birds, located at the bifurcation of the trachea.

SYSTOLE. The contracted condition of the heart and arteries.

TABULAR. A skull bone of early fishes, amphibians, and lower reptiles, just posterior to the parietals.

TALUS. A bone of the proximal row of the tarsus; tibiale, astragalus.

TAPETUM. A layer of the choroid coat of the eye which reflects light in many animals; e.g., in fishes, cat.

TARSAL GLAND. Sebaceous glands in the eyelid; Meibomian.

TARSUS. The ankle.

TASTE BUDS. Groups of cells in which center the sense of taste.

TECTORIAL MEMBRANE. A membrane of the organ of Corti, of the inner ear.

TELENCEPHALON. The anterior region of the forebrain.

TEMPORALIS. An adductor muscle of the mandible.

TENDON. A tough, elastic connective tissue sinew connecting a muscle to its insertion.

TENSOR FASCIA. A superficial muscle of the thigh.

TENTORIUM. A transverse fold of dura mater, sometimes osseous, between the cerebellum and the cerebral lobes; e.g., in cat, dog.

TERES MAJOR and MINOR. Adductors of the humerus.

TERMINALIS. A small cranial nerve, paralleling the olfactory; Pinkus' nerve.

TESTOSTERONE. The testicular or male sex hormone, that maintains the secondary sex characters in males.

TETANY. Spasm of muscles, usually caused by toxin or poison.

TETRAPOD. Vertebrate animal with four limbs.

THALAMUS (OF BRAIN). The side walls of the diencephalon.

THECODONT. Referring to teeth imbedded in sockets.

THORACIC DUCT. A single or paired duct through which the lymph is transferred to the venous system.

THYMUS GLAND. An endocrine gland of the throat region.

THYROHYOID. A muscle of the hyoid and thyroid cartilage.

THYROID CARTILAGE. A large cartilage of the larynx of mammals.

THYROID GLAND. A ductless gland of the neck region.

THYROXIN. Hormone of the thyroid gland.

TIBIA. The inner shin bone.

TIBIALE. A bone of the proximal row of the tarsus, articulating with the tibia.

TRABECULAE. A pair of anterior cartilaginous bars, appearing in the development of the chondrocranium.

TRACHEA. The windpipe.

TRACT FASCICULUS CUNEATUS. A nerve tract on the dorsal side of the spinal cord.

TRACT GRACILIS. A nerve tract on the dorsal side of the spinal cord.

TRANSPALATINE. A bone connecting the pterygoid and maxilla.

TRANSVERSE PROCESS. A lateral process on the neural arch of a vertebra formed by the diapophysis and parapophysis.

TRAPEZIUM. The bone of the distal, carpal row, which is at the base of the first metacarpal; carpal 1.

TRAPEZIUS. A muscle between the scapula and the vertebral column.

TRAPEZOID. A bone of the distal carpal row, which is at the base of the second metacarpal; carpal 2.

TRICEPS. An extensor of the arm.

TRICODONT. Referring to teeth with three cones, parallel to the line of the jaw.

TRICUSPID VALVE. A valve of the heart, between the right atrium and the right ventricle, having three cusps.

TRIGEMINUS. The fifth cranial nerve.

TRIPUS. The large posterior bone of the Weberian ossicles.

TRIQUETRAL. A bone of the proximal row of the carpus articulating with the ulna; ulnare.

TRITUBERCULAR. Referring to teeth with three tubercles on the crown.

TROCHANTER. A process on the femur for muscle attachment.

TROCHLEAR. The fourth cranial nerve.

TROPIBASIC. Referring to a type of skull in which the trabeculae join, just anterior to the hypophysis (in amniotes).

TUBA AUDITIVA. A small tube connecting the cavity of the middle ear with the pharynx in tetrapods; Eustachian tube.

TUBER CINEREUM. A structure on the ventral region of the diencephalon.

TUBERCULAR HEAD (RIB). The secondary head articulating with the diapophysis.

TUBERCULUM IMPAR. An embryonic structure appearing in the development of the tongue.

ULNA. A bone on the mesial side of the forearm.

ULNARE. A bone of the proximal carpal row, articulating with the ulna; triquetral, cuneiform.

ULTIMOBANCHIAL BODIES. Small glands associated with the gill pouches, probably endocrine in function.

UMBILICUS. Scar on the abdomen of mammals, where the navel cord was attached.

UNCINATE. A bone of the distal carpal row, at the bases of the fourth and fifth metacarpals; carpalia 4 + 5.

- UNCINATE PROCESS.** A small overlapping process on the ribs of some reptiles and most birds.
- UNGUICULATE.** Referring to animals with claws.
- UNGULATE.** Referring to hoofed animals, of the division Ungulata.
- UNGULIGRADE.** Referring to animals with hoofs.
- UREA.** A nitrogenous component of urine.
- URETER.** A duct which in amniotes conveys the urine from the kidney to the bladder.
- URETHRA.** A duct which in amniotes conveys the urine from the bladder to the outside of the body.
- URODAEUM.** The part of the cloaca into which the urogenital sinus discharges.
- UROGENITAL SINUS.** A pouch in connection with the urinary and genital systems; the common chamber of the male shark, through which both the sex products and the urine enter the cloaca.
- UROPYGIAL GLAND.** An oil gland at the base of the tail in birds.
- UTERUS.** A specialized region of the oviduct, in which eggs may hatch in lower vertebrates, and young develop in mammals; womb.
- UTRICULUS.** A sac of the inner ear connecting the semicircular canals.
- VACUOLATED.** Filled with small cavities.
- VAGINA.** The posterior end of the oviduct, leading from the uterus or womb to the exterior.
- VAGUS.** The tenth cranial nerve; pneumogastric.
- VALVE OF EUSTACHIUS.** A semilunar fold in the right atrium that covers the entrance of the post cava.
- VALVE OF THEBESIIUS (VALVULA SINUS CORONARI).** Fold covering the opening of the coronary sinus in the right atrium.
- VANE.** The web of a feather.
- VAS DEFERENS.** A duct conveying the spermatozoa.
- VASA EFFERENTIA (EFFERENT DUCTULES).** Tubules connecting the testes with the vas deferens.
- VASOMOTOR NERVES.** Those supplying the walls of blood vessels.
- VENAE ADVEHENTES.** Veins distributing the blood from the renal portal system to the mesonephros.
- VENAE REVEHENTES.** Veins returning the blood from the mesonephros to the posterior cardinals.
- VENTRAL.** Underside or towards the underside.
- VENTRICLE.** A chamber, as the ventricle of the heart, the ventricle of the brain.
- VENTRICULUS.** The muscular stomach, or gizzard, of some reptiles and birds.
- VERMIS.** Median, unpaired part of the cerebellum.
- VERTEBRA.** One of the segments forming the backbone or vertebral column.
- VESICLE.** A small sac or cavity.
- VESTIBULAR NERVE.** A branch of the auditory nerve, which innervates the semicircular canals and parts of the vestibule of the ear.
- VESTIBULE.** A cavity forming an entrance to another, as in the ear.
- VESTIGIAL.** Remains of an ancestral structure which has lost its original function.
- VILLUS.** A small hair-like process; e.g., on the walls of the intestine, chorion, and placenta.
- VISCERAL ARCHES.** Cartilaginous or bony arches developed in the walls of the pharynx to strengthen and support the gills.
- VISCERAL MOTOR FIBERS.** Motor fibers that go to the organs of the body cavity.

VISCERAL POUCHES. Pouches that, in the embryonic stage, arise from the walls of the pharynx, forming visceral clefts.

VISCERAL SENSORY FIBERS. Sensory nerve fibers that innervate the organs of the visceral cavity.

VISUAL PURPLE. A reddish-purple pigment of the retina, in contact with the rods and cones.

VITREOUS HUMOR. A semi-solid, transparent material between the retina and the lens of the eye.

VIVIPAROUS. Producing living young.

VOMER. A plowshare-shaped bone of the nasal region, in the roof of the mouth.

WEBERIAN OSSICLES. A chain of bones, present in some fishes (Ostariophysi), that connects the swim bladder with the brain and ear.

WHARTON'S DUCT. The duct of the submaxillary gland.

WOLFFIAN DUCT. The excretory duct of the mesonephros, which in males may carry sperm.

WOMB. The specialized region of the oviduct in which young may develop; uterus.

XIPHISTERNUM. The posterior segment of the breastbone, or sternum; the xiphoid process.

XIPHOID PROCESS. The xiphisternum.

ZYGAPOPHYSIS. A process on a vertebra for articulation with another vertebra.

ZYGOMATIC BONE. An element forming part of an arch which joins the maxilla with the posterior region of the skull, called jugal or malar.

ZYGANTHUM. Process on posterior region of neural arch of some reptiles.

ZYGOSPHERE. Process on anterior region of neural arch of some reptiles.

ZYGOTE. The fertilized egg, formed by the union of the male and female gametes.

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